INTERTIDAL COMMUNITY DEVELOPMENT ALONG A DISTANCE/AGE

GRADIENT IN A TIDEWATER GLACIAL FJORD

RECOMMENDED:

Howard M. Feder

Chairman, Advisory Committee

Head, Graduate Program in Marine Sciences and Limnology

APPROVED:

Dean, School of Fisheries and Ocean Sciences

Dean of the Graduate School

Date

INTERTIDAL COMMUNITY DEVELOPMENT ALONG A DISTANCE/AGE GRADIENT IN A TIDEWATER GLACIAL FJORD

A

THESIS

Presented to the Faculty of the University of Alaska

in Partial Fulfillment of the Requirements

for the Degree of

MASTER OF SCIENCE

By

Lewis Crook Sharman, Jr., B.S., B.S.

Fairbanks, Alaska

December 1987

ABSTRACT

Glacier Bay has recently undergone rapid deglaciation, exposing new substrates to colonization and biological development. There is a clearly defined increase in marine intertidal community development with substrate age (0-200 y) and distance (0-90 km) from present-day locations of tidewater glacier termini. The objectives of this research were (1) to describe length-of-fjord patterns of intertidal community composition and corresponding gradients of the near-surface marine physical environment and (2) to use this approach to evaluate the relative contributions of substrate age and physical factors to determining the degree of community development. Distance and age were almost perfectly correlated. Intertidal species richness increased linearly with distance/age. Environmental factors can be grouped into those that also varied linearly along this gradient, and those that varied exponentially. Distance from the glaciers and the other linearly correlated marine environmental factors of water temperature, salinity, and suspended particulate nitrogen factors are probably the most important determinants of intertidal community development.

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ACKNOWLEDGEMENTS

Many individuals have contributed to this research, and it could not have been completed without them. I owe my greatest thanks to those who volunteered to assist me with the fieldwork in Glacier Bay - Ann Neville, Chris Fastie, Susan Lentfer, Hank Lentfer, Kathy Coghill, and Suzanne Murray. They worked (and paddled) through rain, headwinds, and 5:00 A.M. tides with cheer and enthusiasm. I thank them for their assistance, their insights, and their companionship.

Terry Chapin has been an unfailing source of support throughout, patiently (and sometimes successfully) teaching me how to do scientific research without often crying. I thank my other committee members, Howard Feder and Peter McRoy, for their ideas and perspective, and for their review of this thesis.

Several other people in Fairbanks generously offered assistance with various phases of this project. Susan Henrichs went well beyond the call of a non-committee member's duty to help me with all aspects related to measuring and understanding suspended particulates in Glacier Bay. Ken Dunton and Ed Brown taught me about algae, Nora Foster helped me with invertebrate identification. Tama Rucker sincerely tried to teach me how to tell barnacle species apart, and Ken Coyle tried to do the same with amphipods. Vera Alexander, John Goering, Ed Brown, Susan Henrichs, Peter McRoy, Terry Chapin, Howard Feder, Steve Whalen, Dave Boisseau, Mark Oswood, and the Institutes of Marine Science and Arctic

Biology generously loaned and contributed equipment and supplies. The Institute of Marine Science supported my use of the CHN analyzer, and supported repair of my refractometer. Don McSheehy and his welder friends constucted quadrats for me. Gil Mimken and John Smithisler contributed expertise and practical advice about instrumentation. Chirk Chu patiently led me through the maelstrom of computer programming and graphics packages. Karen Kincheloe and Don Borchert helped a great deal with figure graphics. Nancy Anderson, Angela Jones, Genelle Tilton, and other members of the secretarial staffs of the Institutes of Arctic Biology and Marine Science were immensely patient and kind as they educated me in the use of word processing equipment and software.

Help also came from sources beyond Fairbanks. Dr. Robert Wilce of the University of Massachusetts kindly identified an assemblage of intertidal benthic filamentous algae. Bruce Wing of the N.M.F.S. Auke Bay Lab sent formalin to Glacier Bay in response to my urgent request. David Duggins of Friday Harbor Labs, University of Washington, and Rich Palmer of the University of Alberta offered invaluable advice during the planning phase of the research. David Duggins suggested the idea of the dowel experiment to measure mechanical disturbance. Paul Miles of Bolt Beranek and Newman, Inc., Cambridge, Massachussetts, generously shared physical oceanographic field data with me. Alaska Airlines supplied *gratis* transport of excess baggage between Fairbanks and Glacier Bay.

My research was financially supported by research assistantships with Terry Chapin and Susan Henrichs, and later by a Resource Fellowship through the Office of the Vice Chancellor for Research and Advanced Study, University of Alaska. The University of Alaska Foundation came through in the nick of time with travel support to get me and a field assistant to Glacier Bay for fieldwork. Additional travel support from the Vice Chancellor's Office and the Department of Marine Sciences and Limnology allowed me to attend national meetings where I was able to present the results of my work and to interact with other researchers in my field.

I owe a special note of thanks to all those Glacier Bay-ites who contributed support of many kinds. Glacier Bay Lodge donated freezer space for my filter samples. I thank Captains Bob Borden and Chuck Kearns and the crew of the M/V Thunder Bay for transporting my kayaks from Seattle to Glacier Bay. Thanks also are due to Captain Jim Luthy and Mate Brad Carlquist of the National Park Service M/V Nunatak for transporting groceries for me from Juneau to Glacier Bay throughout the summer. Glacial sedimentation researchers Ellen Cowan and Jim Duncker (Northern Illinois University) always welcomed us with a tentsite, a hot dinner, and wonderful companionship at McBride Camp whenever we paddled by, and National Park Service backcountry rangers Kim Heacox and Leigh Selig never failed to offer us the same at Goose Cove. Invariably their sharing of late-night conversation, popcorn, and Mystic Mints revived us, and their interest in our work provided a constant source of encouragement. I thank Superintendent Mike Tollefson and Resource Management Specialist Gary Vequist of Glacier Bay National Park and Preserve for allowing me access to Park Service facilities in Bartlett Cove and for authorizing logistical support, use of equipment, and staff assistance. The group of Park Service seasonal employees, both in Bartlett Cove and in the backcountry, are among the finest people I have

ever known. Their boundless hospitality and encouragement throughout the summer added immensely to the pleasure of my research in Glacier Bay, and I owe them thanks which I doubt I will ever be able to fully express.

As always, my parents, even thousands of miles away in Sweet Home Alabama, were unfailing in their encouragement and belief in me. And finally, of course, my ultimate debt of gratitude is to Glacier Bay, for only by her good grace have I been able to learn anything at all.

INTRODUCTION

The classical theory of primary biological succession assumes a major role of time in defining predictable developmental sequences. Through successional time, species assemblages change directionally in composition, diversity, and biomass from the earliest pioneering stages to a mature "climax" community that has high resistance to external perturbations, allowing it to remain essentially unaltered in these respects with subsequent passage of time. The climax community typically has higher diversity and biomass than do early developmental stages (Odum 1969).

Glacier Bay ecosystems are ideal for successional research because the area has been exposed by a rapidly receding complex of tidewater glaciers over the past 200 years. This retreat has been well-documented, allowing researchers to assign ages accurately to substrate surfaces across the 100 km transect from the baymouth up to the present-day locations of glacier termini. The bay's terrestrial communities present a dramatic display of all stages of succession from the very young, relatively unvegetated landscape of the extreme upper inlets to the mature, well-developed 200 y-old spruce/hemlock forest adjacent to the fjord entrance. Studies of terrestrial succession at Glacier Bay have played an important role in the development of successional theory (Cooper 1923a,b,c, Crocker and Major 1955, Lawrence et al. 1967).

Despite the contribution of Glacier Bay to the understanding of terrestrial primary succession, virtually no attention has been given to parallel processes of community development in the marine environment of this system. A preliminary list of species in Glacier Bay marine intertidal communities at several sites (Mueller 1973) suggested that a well-defined gradient in number of species existed along the length of the bay in the marine habitat, parallel to the gradients of substrate age (time since initial exposure by the receding tidewater glaciers) and distance from locations of tidewater glacier termini (Fig. 1).

In other southeastern Alaska glacial fjords there are strong gradients in marine physical factors such as water temperature and salinity between the head of the fjord and the mouth (Pickard 1967). Earlier workers in Glacier Bay have documented, for limited portions of the bay or on a gross scale with a few widely scattered measurements, length-of-fjord patterns in surface water temperature and salinity (Longerich *et al.* 1971, Burrell and Matthews 1974, Malme *et al.* 1982, Miles and Malme 1983, Krieger and Wing 1984) and suspended sediment content (Loder 1971, Hoskin and Mueller 1977). A detailed study of a wide range of physical parameters of the near-surface marine environment has never been undertaken.

The species composition of northern intertidal communities is known to be affected by salinity (Calvin 1977, Cimberg 1982) and ice scour (O'Clair 1981, Cimberg 1982, Keser and Larson 1984). It has been suggested that these and other environmental factors such as water temperature, water clarity, and suspended sediment content are important in determining intertidal community composition in Glacier Bay (Hoskin

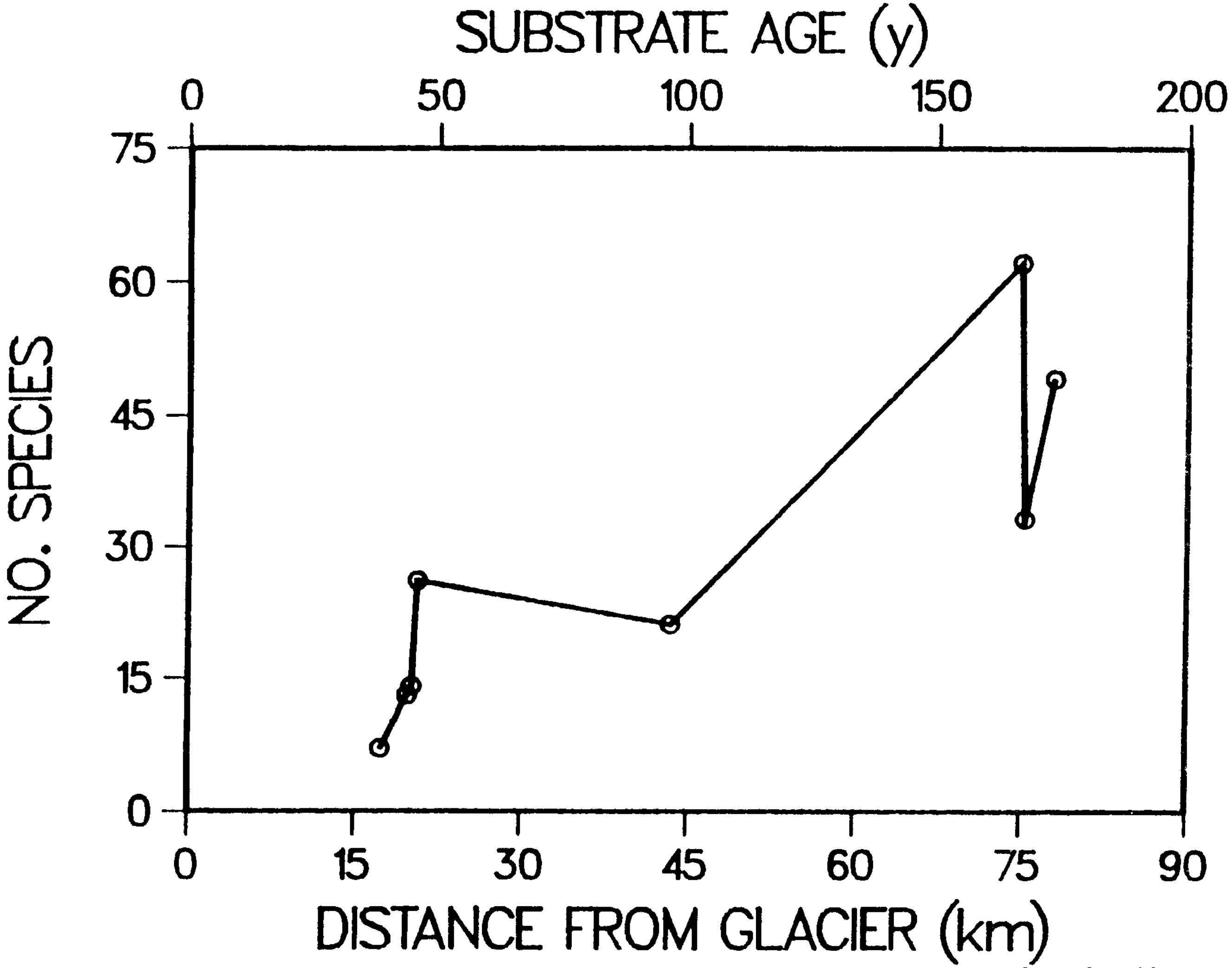


Figure 1. Number of species found in 1971 and 1972 at intertidal sites along the distance gradient from the tidewater face of Muir Glacier to the mouth of Glacier Bay (Mueller 1973). Due to continuing glacial recession, site locations were approximately 5 km closer to the glacier than at present.

and Mueller 1977, Hale and Wright 1979). In addition, Hale and Wright (1979) believe that time since deglaciation (age of substrate) is a potential controlling factor.

Previous experimental studies of marine littoral community development suggest that intertidal succession generally proceeds from bare surface to the mature "climax" stage in five to ten years (Sousa 1979a,b). Sousa described the colonization of artificial or freshly denuded substrates in a marine environment known to have remained relatively unchanged (compared to Glacier Bay) for a long period of time. The level of community development described as "late successional" or "climax" was in fact defined in terms of its similarity to that of the surrounding resident community. Successional sequences were studied over a relatively short timescale during which directional changes in the marine physical environment were considered unimportant. In Glacier Bay, however, patterns of intertidal community development along the 100 km-long gradient of distance from tidewater glaciers also correspond to the 200 y gradient of substrate age, and there is the possibility that succession is occurring over a relatively long timescale which is similar to that of adjacent terrestrial communities. Does the pattern of intertidal community development along the Glacier Bay age and distance gradients represent (a) long-term biological succession or (b) a response to stresses of the marine physical environment controlled by distance from tidewater glaciers?

Because the ages of sites are known, Glacier Bay provides a unique opportunity to determine the relative importance of time since deglaciation and characteristics of the physical environment in controlling patterns of marine intertidal community development. The objective of this study was to investigate those relationships by quantitatively describing intertidal communities in Glacier Bay and the associated physical factors of the ambient marine environment.

STUDY AREA

Glacier Bay is the dominant geomorphic feature of Glacier Bay National Park and Preserve, located near 58°50' N lat. and 136°00' W long. in southeastern Alaska (Fig. 2). It is a classic example of a high latitude, glacially eroded, silled, estuarine fjord system (Syvitski *et al.* 1987). The 100 km, two-armed fjord has steeply walled, deep (250-400 m) basins separated by shallow sills. The terminal moraine lies immediately outside the mouth of the fjord at 65 to 70 m depth, while the major sill is at the same depth approximately ten km inside the mouth. Most of the inlets have their own sills; the Muir Inlet sill at the base of the eastern arm is 60 m deep. The main trunk of the bay opens into Icy Strait, thence to the open North Pacific Ocean approximately 35 km to the west.

The local region was overlain by glacial ice as recently as 1780, but the trunk glaciers have retreated 15 times more rapidly than glaciers anywhere else in the world in recent times (Lawrence 1958) to expose the present fjord system. The history of this retreat has been well-documented, particularly over the last 100 years; selected known past locations of tidewater glacier termini are shown in Figure 2. Muir Glacier, at the extreme end of the eastern arm of the bay, has been retreating at an average rate of 0.41 km/y since 1860; Riggs Glacier (closest to Muir Glacier in Fig. 2) has joined Muir in a retreat averaging 0.12 km/y since 1945 and 0.25 km/y since 1960 (Mackiewicz *et*

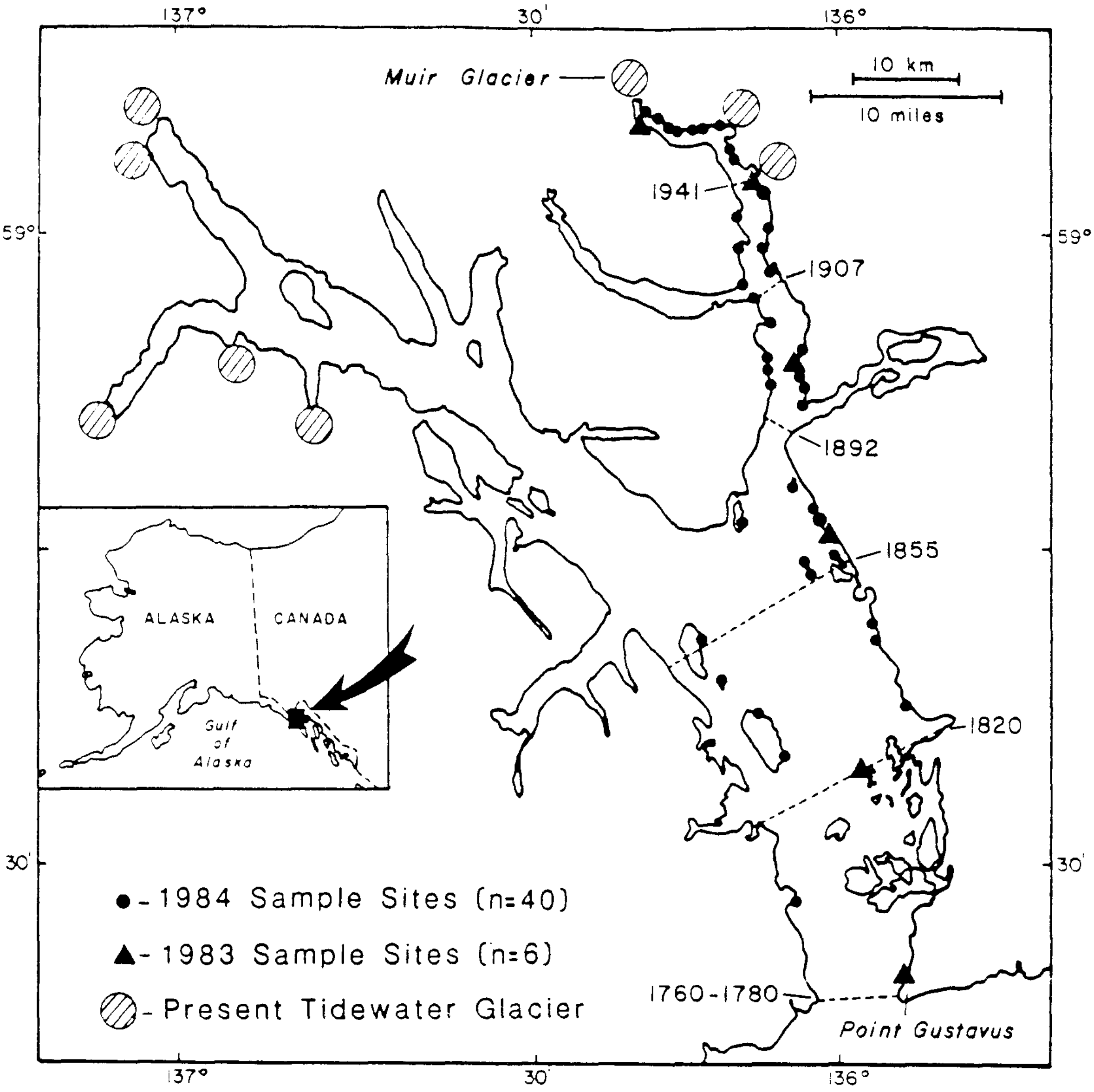


Figure 2. Glacier Bay, Alaska, showing locations of historical (dashed lines) and present tidewater glacier termini, forty 1984 study sites, and six 1983 study sites (same as sites for 1984 dowel experiment). Note location of Muir Glacier at the extreme head of the eastern arm. Icy Strait is immediately outside the fjord mouth.

al. 1984). Maximum rates of retreat as high as 2.4 km/y have been measured (Powell 1980). Associated with glacial retreat in Glacier Bay is isostatic rebound of the land surface at a rate of approximately two cm/y. Assuming a constant rate of rebound, the current land surface has risen from the sea a total of over 3.5 m during the past 200 years. Rebound occurs more rapidly with increasing distance from present glacier termini; the rebound rate of approximately four cm/y at the mouth of Glacier Bay was the highest rate in southeastern Alaska two decades ago (Hicks and Shofnos 1965).

Glacier Bay is surrounded by high mountains (to 4600 m) harboring extensive icefields which are the sources of the tidewater glaciers entering the fjord. Regional topography coupled with proximity to large Aleutian low-pressure atmospheric systems over the adjacent Gulf of Alaska determines the climatic regime of the area. The climate of Glacier Bay has been summarized by Goldthwait *et al.* (1966), McKenzie (1966), and Streveler (1971). It is generally characterized as maritime, with relatively narrow daily and seasonal temperature ranges, abundant precipitation, persistent cloudiness, and high relative humidity. The area experiences cool summers and mild winters, generating temperatures that average 13 and 4°C, respectively. Summer temperatures in the inner bay average 2 to 3°C cooler than those of the outer bay. Precipitation is strongly seasonal; May and June are the driest months, while September through November are the wettest months. Occasionally violent storms with high winds occur during autumn. Mean precipitation for the area is 190 cm/y, the majority of which falls as rain.

The oceanography of Glacier Bay is characteristic of glacial fjords in Alaska. Water column properties are seasonally variable. During summer/fall (June-September) the water column becomes strongly stratified with brackish water overlying more saline water. This stratification breaks down during winter/spring (November-February), and a homogenous condition develops, while freshwater input is at a minimum, and bottom water renewal from Icy Strait occurs (Quinlan 1970, Matthews and Quinlan 1975).

An estuarine-type circulation becomes established during the spring and summer. Large quantities of fresh water (mostly meltwater) enter the fjord at the heads of inlets with the annual runoff peak in May. As the brackish surface flow travels seaward, it entrains underlying water. By continuity of volume, this water is replaced by return flow in the opposite direction (up-fjord) of higher density water at depth (Quinlan 1970, Burrell and Matthews 1974, Matthews and Quinlan 1975, Hale and Wright 1979). Matthews and Quinlan (1975) believe that the glacial ice in Muir Inlet acts mainly as a heat sink and freshwater source, maintaining a low-level estuarine circulation even during winter months with low surface runoff.

The region experiences a semi-diurnal tidal regime, with a tidal period of approximately 12.4 hours. Vertical tidal ranges are high within Glacier Bay, averaging 4.5 m for the year and occasionally exceeding 6 m during bi-monthly spring tides. Mean annual tidal ranges are approximately 5 m for the outer bay and 4.25 m for the eastern arm of the inner bay comprising Muir Inlet (Mackiewicz *et al.* 1984). With over 650 km of shoreline, Glacier Bay has an extensive intertidal zone.

The intertidal exhibits clear vertical zonation (Duggins and Quinn 1979, Hale and Wright 1979). A wide variety of intertidal habitats occurs in Glacier Bay, including solid bedrock outcrops and unconsolidated substrates ranging from large boulders to mudflats. Species composition is typical of glacial fjords throughout southeastern Alaska (Mueller 1973).

MATERIALS AND METHODS

Although the bulk of the research was carried out during the summer of 1984, preliminary measurements of physical characteristics of the near-surface marine environment were made during two visits in late August and early September 1983, to six sites. These sites were evenly spaced along a transect from the baymouth to within two km of the terminus of Muir Glacier, the largest and most active tidewater glacier in the eastern arm of Glacier Bay (Fig. 2). During this preliminary 1983 study period I also made reference collections of intertidal plants and animals that were later identified in Fairbanks.

The 1984 research was conducted along the same transect of substrate age and distance from Muir Glacier as the 1983 work. Forty study sites were selected on consolidated bedrock outcrops in the intertidal zone and were approximately equally distributed along the transect (Fig. 2). Sites were chosen so that they were as similar as possible in terms of rock type, beach slope, exposure to wavewash, and proximity to freshwater streams. Each site was examined once during the study, early June through late August, 1984. To ensure that summer seasonal changes in measured variables did not confound the natural gradient, I made six trips, each approximately two weeks apart, from baymouth to glacier and examined approximately seven sites, spaced along the entire transect, during each trip. The 1984 research was conducted entirely *via* kayaks.

Environmental Parameters

For each site, the time since initial exposure was calculated using known terminus locations from the historical record (Powell 1984). In addition, distance along the bay from the current Muir Glacier terminus was measured. At each of the six sites visited in 1983, I measured nearshore surface water temperature (to nearest 0.5°C with standard mercury thermometer), salinity (to nearest 1.0‰ with American Optical temperature-compensated refractometer), and turbidity (depth in m of 30-cm Secchi disc disappearance). Means were calculated for measurements from both visits to each site.

The 1984 research was considerably more extensive because it was necessary to more completely describe the environment to which the intertidal was exposed. Beach characteristics were of interest, as well as characteristics of the water column from the surface to the depth equaling the maximum tidal excursion. Slope, aspect, and air temperature immediately adjacent to the shaded rock surface were recorded for each site, using inclinometer, compass, and standard mercury thermometer, respectively. The marine environment was examined by collecting seawater samples with a 2-L Van Dorn bottle from depths of 0, 2.5, 5, and 7.5 m at each site, within 50 m of shore. Hereafter, "near-surface" will refer to measurements from those samples that form the basis for descriptions of marine environmental parameters. Samples were collected during the flood portion of the tidal cycle, 1.5 to 4 h after low tide, and analyzed for water temperature and salinity using the same procedures as in 1983. Appendix I is an example of a field data sheet.

Aspects of the suspended particulate regime also were measured quantitatively. Known sample water volumes (generally 300-500 ml) were filtered through pre-weighed Millipore 0.45 μ membrane filters using a standard filtering apparatus with a hand vacuum pump. The filters were later oven-dried at 60°C for 20 h and re-weighed to determine amount of total suspended particulates. Twenty percent of the samples were collected as replicate pairs.

At 26 of the 40 sites, volumes of seawater equal to those filtered for total suspended particulates from a given depth were filtered through pre-combusted (425°C for 3 h) Gelman type A-E glass-fiber filters. Filters were transported in clean plastic Petri dishes and returned to the dishes after filtration. Water was drawn from the same bottle samples used for measurement of total suspended particulates. Approximately 20% of these samples were collected as replicate pairs. To prevent biological activity, samples were treated with four drops formalin solution (40% formaldehyde) on the filter immediately following filtration. The filters were kept in the dark at ambient temperatures for up to 12 days before being frozen for storage. During January and February, 1985, filters were analyzed for particulate carbon (C) and nitrogen (N) using a Perkin-Elmer model 240-C elemental analyzer. Immediately before analysis the filters were thawed, wrapped in pre-combusted aluminum foil, and oven-dried at 105 to 110°C for at least 40 hours. Filters were not acid-treated prior to analysis because findings by other workers (see page 86) indicated that naturally occurring amounts of $CaCO_3$ were negligible. Clean pre-combusted filters with four drops formalin added were wrapped and dried as above and run as blanks (n = 20), and mean blank values for C and N were subtracted from values for each field sample. Again, replicate samples were collected for approximately 20% of all samples. The elemental analyzer measured absolute amounts (μg) of C and N in the samples. Carbon:nitrogen ratios were calculated from these values.

Percentages C and N of total suspended particulates by weight were calculated by dividing the C or N content of the glass-fiber samples by the corresponding weight of total suspended particulates from Millipore filters. Particulates on both filter types were collected from the same bottle sample for each depth at a site. Mean pore sizes of the two filter types were different (slightly smaller for Millipore filters), so particulate retention levels also were different, but I believe that data from the two filter types may be reasonably combined for the purpose of comparisons across sites. Because Millipore filters retained more particulates from a given volume of water than did glass-fiber filters, the calculated values for percentages C and N of total suspended particulates by weight were conservative but still should indicate overall patterns of change among sites.

Water turbidity at each site was described in terms of the average vertical extinction coefficient k, a value calculated by integrating submarine light intensities measured at every meter through the water column from the surface through 8 m by the equation:

$$I_z = I_0 e^{-kz} \quad ,$$

where I_O is the incoming light intensity at the sea surface and I_z is the light intensity at depth z (Parsons *et al.* 1977).

The maximum depth of the euphotic zone, where phytoplankton photosynthesis is equal to respiration, is referred to as the compensation depth and is commonly assumed to be the depth at which there is 1% of the surface illumination (Parsons *et al.* 1977). This depth was calculated for each site using the previously described integrations of light extinction through the water column to the depth at which it was 1% of the value measured at the surface.

Light measurements were taken within 50 m of shore, 2.5 to 4.5 h after low tide, using a LI-COR model LI-185 light meter with a LI-COR model LI-192 underwater quantum sensor that measures photosynthetically active radiation (400 through 700 nm). These measurements were used to calculate extinction coefficient and 1% light depth.

To measure potential ice scour, grounded ice fragments ≧ 0.1 m greatest diameter, as well as those fragments floating within 3 m of shore, were counted at low tide along a 100-m length of shoreline at each site. An experiment to more directly measure relative levels of mechanical disturbance was begun in late May, 1984. Thirty 1.5-cm wooden dowels, 3 mm in diameter, were cemented end-on with marine epoxy putty onto boulder surfaces in the intertidal zone at each of six permanent sites (the same sites sampled in 1983) spaced approximately 20 km apart along the transect (Fig. 2). At each site, three rows of ten dowels each were installed at vertical intertidal levels of 2, 3.5, and 5 m above mean lower low water (MLLW). Rows were laid out parallel to the shoreline, and individual dowels within a row were separated by 0.2

m. Three months later, in late August, dowel arrays were relocated, and remaining undamaged dowels were counted at each site so that levels of mechanical disturbance could be compared among sites.

Biological Community

The intertidal biological community at each site was described during low tide at standard vertical heights of 0, 1.25, 2.5, 3.75, and 5 m above MLLW. Locally corrected tide tables (NOAA 1984) were used in locating these vertical levels at each site (and the previously described dowel levels) by sighting through a spirit level from the edge of the water at low tide to a survey staff at the standardized heights. The 0 m intertidal height was described at only 30 of the 40 sites because the tide was not always low enough to expose that zone on the dates of my visits.

At each vertical level, ten 0.1 m^2 quadrat frames were placed at random, non-overlapping locations along a 10 m-long transect parallel to the shoreline. Percent substrate coverage was visually estimated for each species of intertidal plant and animal; also estimated were percent unoccupied (bare rock) surface, and percent surface covered by $\geqq$ 0.5 cm glacial silt (a component of percent unoccupied surface). Abundance (number of individuals per 0.1 m^2 quadrat) was recorded for rare or mobile animal species. Where *Littorina sitkana* and *Collisella* spp. were extremely abundant, they were subsampled from a 100 cm^2 quadrat placed in the upper left corner of the larger quadrat. Coverage and abundance data were combined for certain statistical purposes. For those cases the combined data will be referred to as "coverage/abundance" so that it can be contrasted with frequency (percent occurrence of a species in the total number of quadrats at a site) data. Authorities most frequently used for taxonomic nomenclature were Smith and Carlton (1975) for animals and Abbott and Hollenberg (1976) for algae.

Statistical Analyses

For each intertidal height at each site, means and standard errors were calculated for the overall species richness (number of species per 0.1 m^2 quadrat), percent unoccupied surface, and percent silt, as well as the percent coverage or abundance for individual species. Means were also calculated for measurements of the physical parameters of the water column. A principal components analysis (PCA) routine (Dixon *et al.* 1981) was performed using site means for all species frequency and coverage/abundance data at each intertidal height to determine whether there were distinct groupings of communities along the transect. Similarly, PCA of environmental factors was performed to determine groupings of physical variables that showed similar patterns of variation among sites (air temperature and 1% light depth were not included in the analysis). Linear, polynomial, and exponential regression analyses (Dixon *et al.* 1981) were used to examine the relationship of distance from the glacier (and substrate age) to each environmental parameter. Stepwise multiple regression analysis (Dixon *et al.* 1981) was then used to determine which of the environmental parameters (excluding air temperature and 1% light depth) correlated most strongly with coverage/abundance of each species at each intertidal level. Similarly, stepwise regressions were performed for species richness, percent unoccupied surface, and principal component scores (derived from PCA of the biological data) for each intertidal level.

RESULTS

Physical Environment

Substrate age increased linearly ($r^2 = 0.99$; $p < .001$) with distance from the present-day terminus of Muir Glacier for the 40 study sites occupied in 1984 (Fig. 3). Consequently, biological and physical parameters were as well correlated with distance from the glacier as with substrate age. Except for short periods of very rapid retreat approximately 125 y ago (*ca.* 1860), 80 y ago (*ca.* 1905), and 20 y ago (*ca.* 1965) the overall rate of glacial retreat (approximately 2.3 km/y) has been remarkably constant.

I. Hydrography

In 1983, surface water temperature (range 5-13°C) and surface salinity (range 7-28‰) increased from glacier to baymouth (Figs. 4a,b; Appendix II). Surface water temperature steadily increased with distance along the gradient (Fig. 4a), while surface salinity increased to a constant 26‰ approximately 70 km from the glacier (Fig. 4b).

In 1984, near-surface water temperature and salinity increased linearly from glacier to baymouth (Fig. 5a,b), with water temperature increasing from 5 to 11°C, and salinity increasing from 15 to 31‰ along the transect. If only surface measurements (Appendix III) are

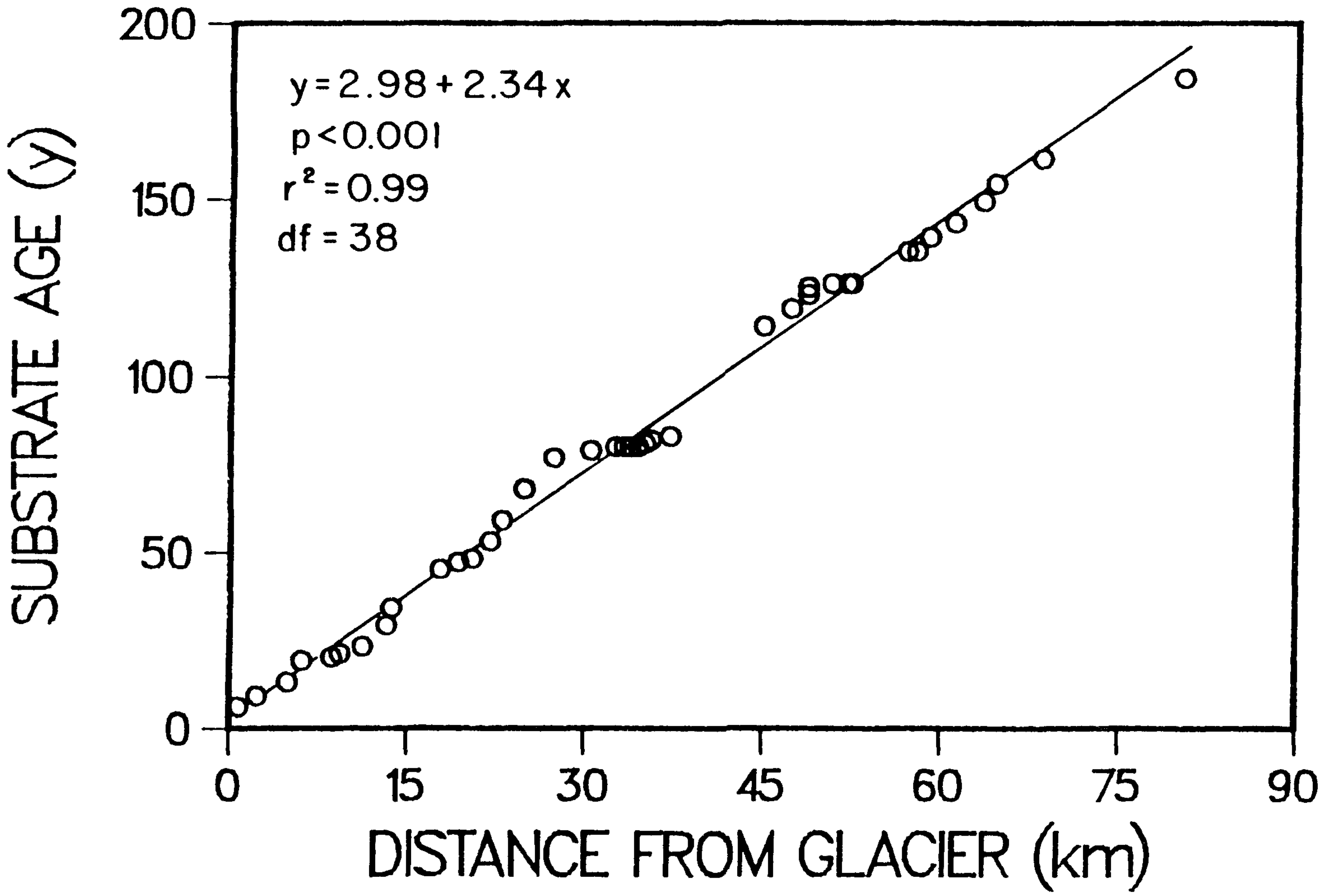


Figure 3. Relationship of substrate age to distance from Muir Glacier for the forty 1984 study sites.

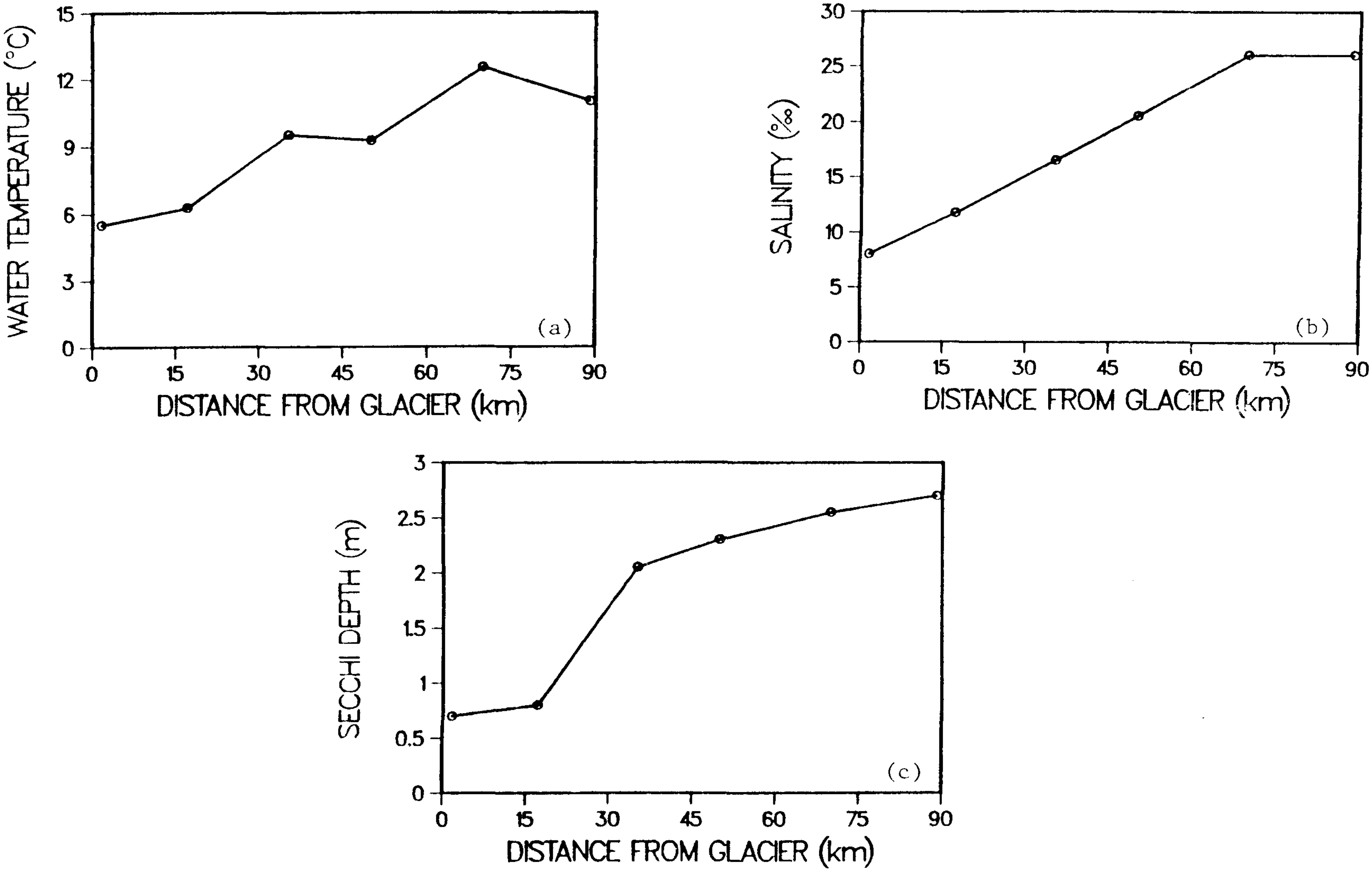


Figure 4. Relationships of marine environmental parameters to distance from Muir Glacier for six 1983 study sites: (a) surface water temperature, (b) surface salinity, and (c) Secchi depth.

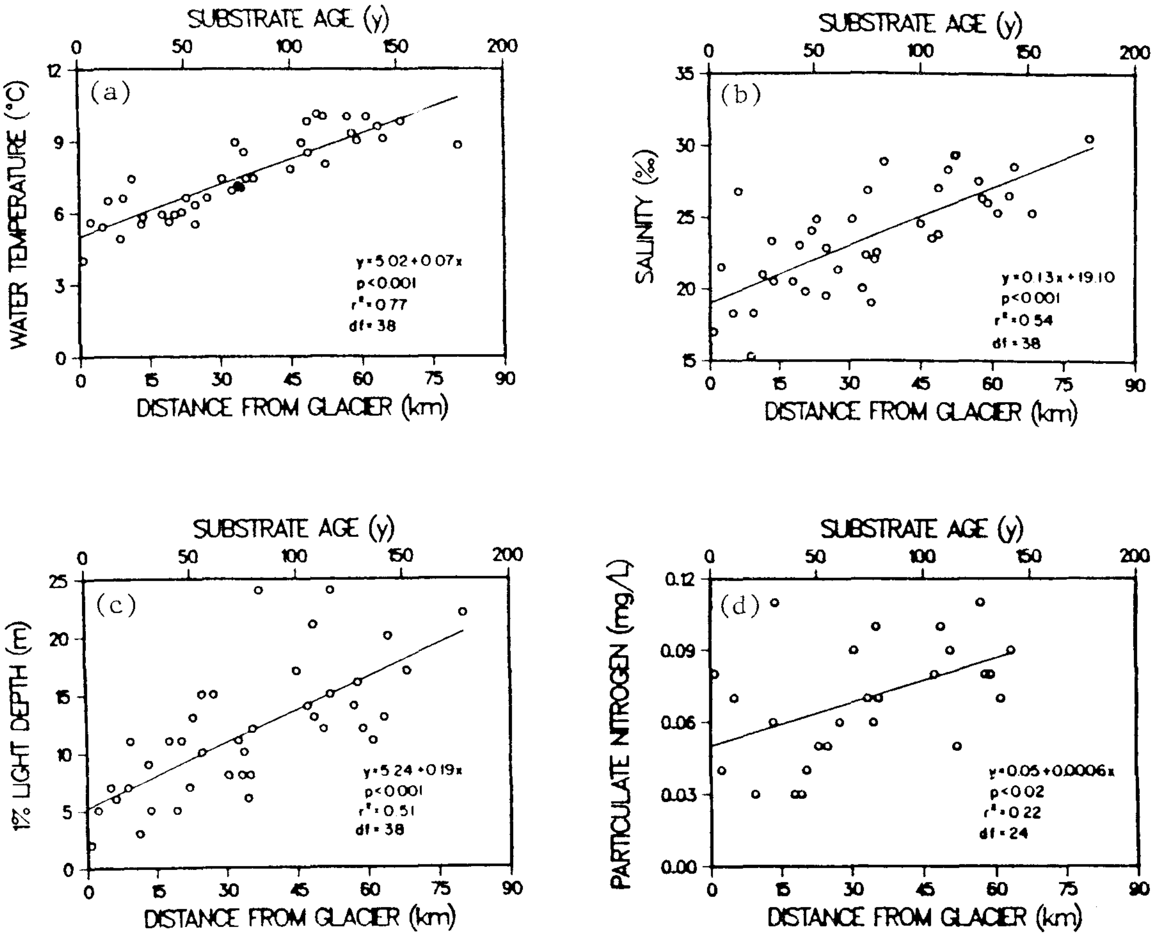


Figure 5. Relationships to distance from Muir Glacier and substrate age shown by near-surface (a) water temperature, (b) salinity, (c) 1% light depth, and (d) suspended particulate nitrogen concentration in seawater. Values in (a), (b), and (d) are means of measurements made at depths of 0, 2.5, 5, and 7.5 m. n = 40 sites except for (d) where n = 26 sites.

considered, these 1984 ranges and trends agreed well with 1983 results (Figs. 4a,b; Appendix II).

In addition to horizontal gradients related to distance from the glacier and substrate age, there were vertical patterns. Water temperature usually (65% of all sites) decreased with depth (Appendix III). This trend appeared most consistently in the outer bay, beyond 50 km from the glacier. A contrasting increase in temperature with depth occurred at sites very near the glacier. Temperatures from lower depths varied much less among sites than did surface temperatures.

Salinity consistently increased with depth at almost all (90%) sites (Appendix III). Vertical increases were much more pronounced in the inner bay (two- to three-fold increases over surface salinities) out to approximately 35 km from the glacier; beyond this distance increases in salinity with depth declined to usually less than 25% above surface values. As with water temperature, the greatest variation in salinity among sites was in surface measurements. Even at sites very close to the glacier, salinities at 7.5 m were 25‰ and increased only up to 31‰ all the way out to the baymouth. These vertical water temperature and salinity patterns are consistent with the physical oceanographic principle of colder, more saline water of higher density being overlain by warmer, less saline water of lower density (Pond and Pickard 1983).

Air temperature increased slightly with distance from the glacier (Fig. 6c), presumably because of the cooling effect of the large ice mass. Temperatures ranged from 7°C close to the glacier to 17°C toward the mouth of the bay. Air temperatures fluctuated daily with changing weather at all locations along the transect.

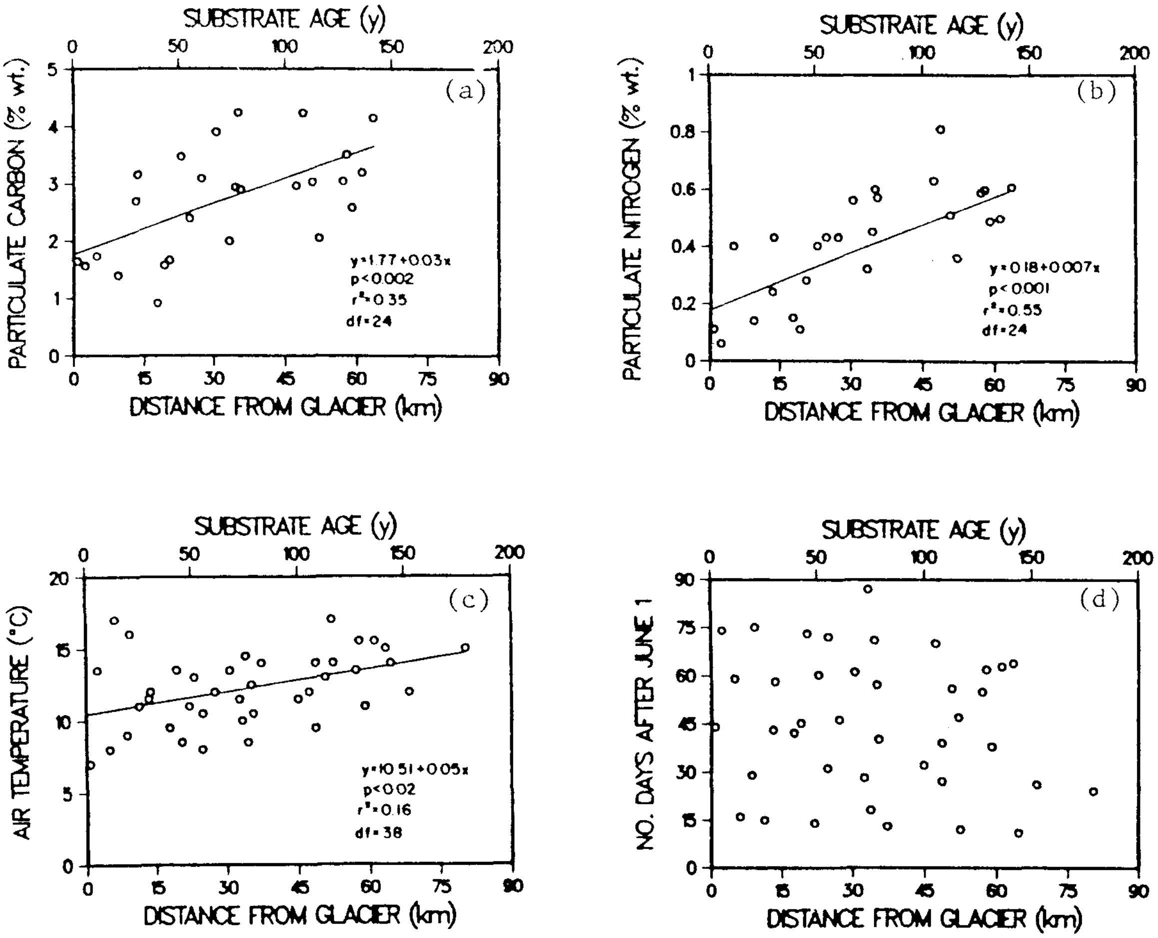


Figure 6. Relationships to distance from Muir Glacier and substrate age shown by near-surface (a) percent weight suspended particulate carbon per total suspended particulates, (b) percent weight suspended particulate nitrogen per total suspended particulates, (c) air temperature at intertidal surface, and (d) sampling date (number of days after June 1). For (a) and (b), values are means of measurements made at depths of 0, 2.5, 5, and 7.5 7.5 m, and n = 26 sites; n = 40 sites for (c) and (d). Relationship in (d) is nonsignificant at α = 0.05 (p = 0.38).

II. Suspended particulates

In contrast to the linear increases (with distance) of substrate age, water temperature, salinity, and air temperature, the amount of total suspended particulates decreased exponentially (maximum 159 - minimum 10 mg/L seawater) across the 15 km closest to the glacier (Fig. 7a). Beyond 15 km, amount of suspended particulates reached a relatively low and constant level of approximately 18 mg/L.

Vertical trends of suspended particulates also occurred (Appendix IV) but were less obvious than those of water temperature and salinity. The amount of total suspended particulates by weight per volume of seawater decreased with depth at approximately 45% of the sites sampled. Increases were observed at 12% of the sites, and the remaining 43% of the sites showed no consistent directional pattern with depth.

Thirty two (20%) of the 160 total suspended particulate load measurements were means of replicate pairs. Replicates from the same depth at a site were taken from the same bottle sample and were thus analytical replicates of within-bottle water rather than true field sampling replicates. For all 32 replicate pairs, the overall mean of the deviations from the individual means was 3.7%. The five highest deviations for individual replicate pairs were 13.3, 11.1 (three pairs), 10.0, 8.1, and 7.0% respectively. It is expected that replicates from separate bottle samples from the same depth at a site would have exhibited significantly greater variability. However, a mean deviation from individual means of only 3.7% indicates that most of the variation

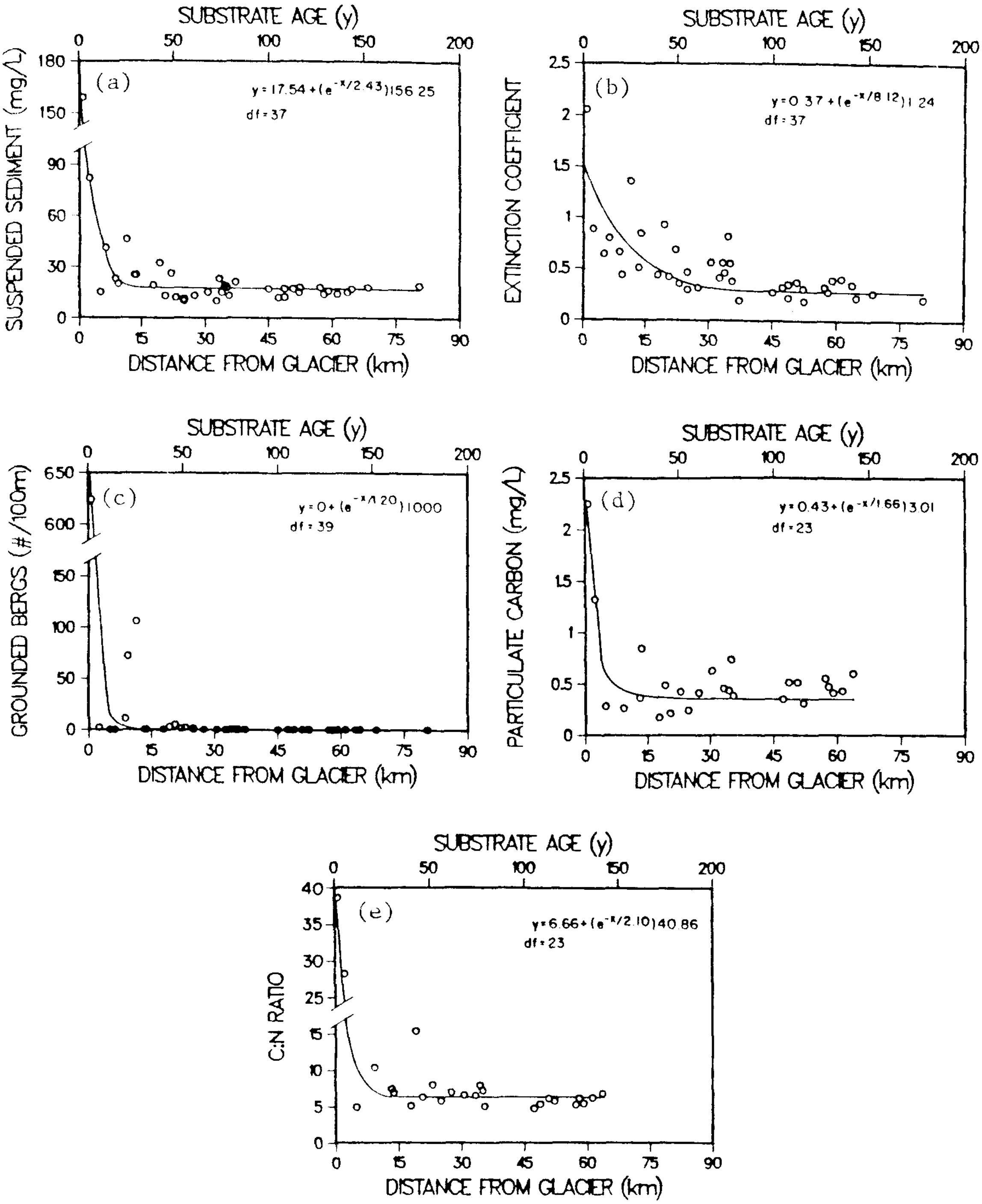


Figure 7. Relationships to distance from Muir Glacier and substrate age shown by near-surface (a) total suspended particulate concentration in seawater, (b) extinction coefficient, (c) number of grounded ice fragments (= bergs), (d) suspended particulate carbon concentration in seawater, and (e) C:N ratio of total suspended particulates. For (a), (d), and (e), values are means of measurements made at depths of 0, 2.5, 5, and 7.5 m. n = 40 sites except for (d) and (e) where n = 26 sites.

in measurements of total suspended particulates was due to site rather than analytical variability.

Total particulate nitrogen (N) in the near-surface water column, and percent (on a weight basis) of carbon (C) and N in total suspended particulates increased linearly with increasing distance from the glacier (Figs. 5d, 6a,b), reflecting reduced suspended mineral material away from the glacier. Predicted (by regression) values for these three parameters at the extreme ends (where no measurements were taken) of the glacier to baymouth gradient range from approximately 0.05 to 0.11 mg/L, 1.8 to 4.3%, and 0.18 to 0.77%, respectively. All three parameters were highly correlated with one another ($r > 0.90$; Table 1) and formed a "group" (PC2; Table 2) in the principal components analysis (see page 86). By contrast, plots of total particulate C (Fig. 7d) and C:N ratios (Fig. 7e) included high values (1.32-2.25 mg/L and 28.2-38.6, respectively) very close to the glacier but showed no directional trend beyond ten km (averages were 0.4 mg/L and 6.7, respectively). These two parameters were highly correlated ($r = 0.93$; Table 1) and formed a "group" (PC1; Table 2) in the principal components analysis (see page 86).

Variability was high among all these particulate relationships, as reflected by their generally low coefficients of determination (Figs. 5d, 6a,b). Such high variability is due to natural variation in fjord environments in terms of both temporal and spatial patchiness (timing and locations of phytoplankton blooms, storms, stream discharge, *etc.*). Relatively small sample sizes, field sampling error, sample contamination, and laboratory analysis error also play a role.

Table 1. Correlation matrix of all environmental parameters measured (including sampling date and excluding air temperature and 1% light depth) for 40 sites. Values are coefficients of correlation (r) between corresponding row and column parameters. Values in suspended particulate carbon and nitrogen categories are based on measurements from 26 sites. The lower portion of the table is the continuation of the right-hand portion of the matrix.

Table 1.

Physical Parameter	Substrate Age	Dist. fr. Glacier	Sampling Date	Slope	Aspect	Water Temp.	Salinity	Tot. Partic. mg/L	Partic. C mg/L	Partic. N mg/L	C:N Ratio	Partic. C % wt.
Substrate Age	1.000											
Dist. fr. Glacier	0.996	1.000										
Sampling Date	-0.136	-0.144	1.000									
Slope	0.098	0.119	-0.132	1.000								
Aspect	-0.277	-0.263	-0.128	0.033	1.000							
Water Temp.	0.875	0.876	0.027	0.029	-0.206	1.000						
Salinity	0.731	0.733	-0.377	0.153	-0.039	0.688	1.000					
Tot. Partic. mg/L	-0.449	-0.445	-0.013	-0.187	0.116	-0.432	-0.301	1.000				
Partic. C mg/L	-0.272	-0.278	0.473	-0.341	0.129	-0.205	-0.309	0.761	1.000			
Partic. N mg/L	0.062	0.058	0.673	-0.370	0.163	0.239	-0.114	0.049	0.637	1.000		
C:N Ratio	-0.402	-0.406	0.454	-0.278	0.074	-0.364	-0.385	0.818	0.930	0.411	1.000	
Partic. C % wt.	0.149	0.139	0.713	-0.337	0.028	0.309	-0.073	-0.116	0.510	0.927	0.322	1.000
Partic. N % wt.	0.252	0.241	0.637	-0.258	0.081	0.413	-0.011	-0.259	0.348	0.901	0.137	0.957
Extinc. Coeff.	-0.642	-0.631	0.057	-0.321	0.103	-0.554	-0.534	0.852	0.636	0.101	0.672	-0.051
No. Ice Frag.	-0.320	-0.320	-0.019	-0.176	0.113	-0.350	-0.340	0.880	0.692	0.096	0.703	-0.045

Physical Parameter	Partic. N % wt.	Extinc. Coeff.	No. Ice Frag.
Partic. N % wt.	1.000		
Extinc. Coeff.	-0.183	1.000	
No. Ice Frag.	-0.142	0.771	1.000

Table 2. Results of principal components analysis of all environmental parameters measured (including sampling date and excluding air temperature and 1% light depth). Column values are coefficients of correlation (*r*) between principal component (PC) and corresponding physical variable. Correlation coefficients with absolute values < .500 (except slope) have been omitted for clarity. An eigenvalue reflects the relative proportion of the total variance within the data set that is accounted for by a PC (*i.e.*, the quantitative relationships among eigenvalues are identical to those among corresponding values of percent total variance explained). For example, an eigenvalue of 1.00 would explain the same amount of variation as would one of the original input variables on the average (in this case, 1/15 or 6.7% of the total variance in the data set).

Table 2.

Physical Parameter	PC1	PC2	PC3	PC4
Total Suspended Particulates (mg/L)	.952			
Number Grounded Ice Fragments	.907			
C:N Ratio	.828			
Particulate Carbon (mg/L)	.821	.509		
Extinction Coefficient	.789			
Particulate Carbon (% total particulate weight)		.970		
Particulate Nitrogen (% total particulate weight)		.939		
Particulate Nitrogen (mg/L)		.938		
Sampling Date		.821		
Distance from Glacier			.938	
Substrate Age			.937	
Water Temperature			.875	
Salinity			.846	
Aspect				.967
Slope		-.353		
Eigenvalue	5.83	4.12	1.89	1.10
Total Variance Explained (%)	38.8	27.5	12.6	7.3
Cumulative Total Variance Explained (%)	38.8	66.3	78.9	86.2

Suspended particulate C and N measured on a weight per volume basis both decreased with depth at 40% of the sites sampled, increased at 5% of the sites, and showed no clear directional change at the other 55% of the sites. The same pattern was observed for suspended particulate C on a percent weight of total suspended particulates basis. Particulate N (percent weight) decreased with depth at 35% of the sites sampled, increased at 25% of the sites, and showed no change at the remaining 40%. Carbon:nitrogen ratio decreased with depth at approximately half the sites, increased at 20%, and showed no clear vertical change at the other 30%.

In general, all measured parameters of the near-surface suspended particulate regime tended to decrease with increasing depth at approximately 40% of the sites sampled; the majority of sites showed no clear vertical trends, while increases with depth were observed at 5 to 25% of the sites. There were no obvious patterns among sites along the horizontal distance/age gradient in relative amounts of vertical variation in these measurements.

For the 20 filter blanks with formalin added, the overall mean blank for C was 75.8 μg (SE = 2.2); the mean blank for N was 1.6 μg (SE = 0.2). These mean blank values were subtracted from all data for formalin-treated filters. Twenty (19.2%) of the 104 sets of particulate C and N values were means of replicate pairs, which were analytical replicates as described previously. For all 20 replicate pairs, the overall mean of the deviations from the individual means was 13.0% for C and 9.1% for N. Four of the 20 pairs for C (three of 20 for N) had deviations of more than 20%. As before, it is expected that replicates from separate bottle samples would have exhibited significantly greater variability. The mean deviations of C and N from individual means were greater than the mean deviation for total suspended particulates, but much less than site-to-site variability.

III. Light

In 1983, turbidity as measured by Secchi depth was high close to the glacier but began rapidly decreasing between 15 and 30 km from the glacier (range 0.6-2.7 m; Fig. 4c; Appendix II).

In 1984, water turbidity as measured by extinction coefficient correlated closely with total suspended particulates (r = 0.85; Table 1), and the curves of exponential decay along the distance/age gradient were quite similar (Figs. 7a,b). Extinction coefficients rapidly decreased across the 25 km closest to the glacier (maximum 1.354) to a relatively low and constant value of approximately 0.400. The general trend of this gradient agreed well with the Secchi depths measured in 1983 (Fig. 4c).

The 1% light depth increased linearly from glacier to baymouth (Fig. 5c) with values ranging from 2 to 24 m as water transparency became greater with decreasing turbidity (Appendix III).

IV. Disturbance

Number of grounded ice fragments decreased exponentially with distance from the glacier, with over 600 fragments counted at the site closest to the glacier terminus (Fig. 7c). Ice fragments are continually calved off the active tidewater faces of the glaciers and are slowly transported seaward by the net surface outflow of low-density fresh water entering at the head of the fjord. The majority of these fragments melt by the time they have traveled 25 km; I encountered no ice at sites beyond this distance.

Relative intensity of mechanical disturbance of the intertidal zone is further described by results from the dowel experiment (Fig. 8; Appendix V). Of the 30 dowels placed at the site closest to the glacier (site A; Figs. 2, 8) in late May, 1984, only two remained three months later in late August. This site, less than two km from the active tidewater face of the glacier, was within the area of highest numbers of grounded ice fragments counted at low tide (Fig. 7c). At site D, located approximately halfway between the glacier and the baymouth, however, all 30 dowels were found still in place. This site was relatively well protected from forms of mechanical disturbance. At the site closest to the mouth of the bay (site F), 14 dowels from the two upper rows remained, but the lower row of dowels could not be located (probably because the tide was not low enough to expose them on the date of the late August visit). If dowels from this row were lost at approximately the same rate as those from higher intertidal levels as was the case at the other sites, a total of 21 of the original 30 dowels

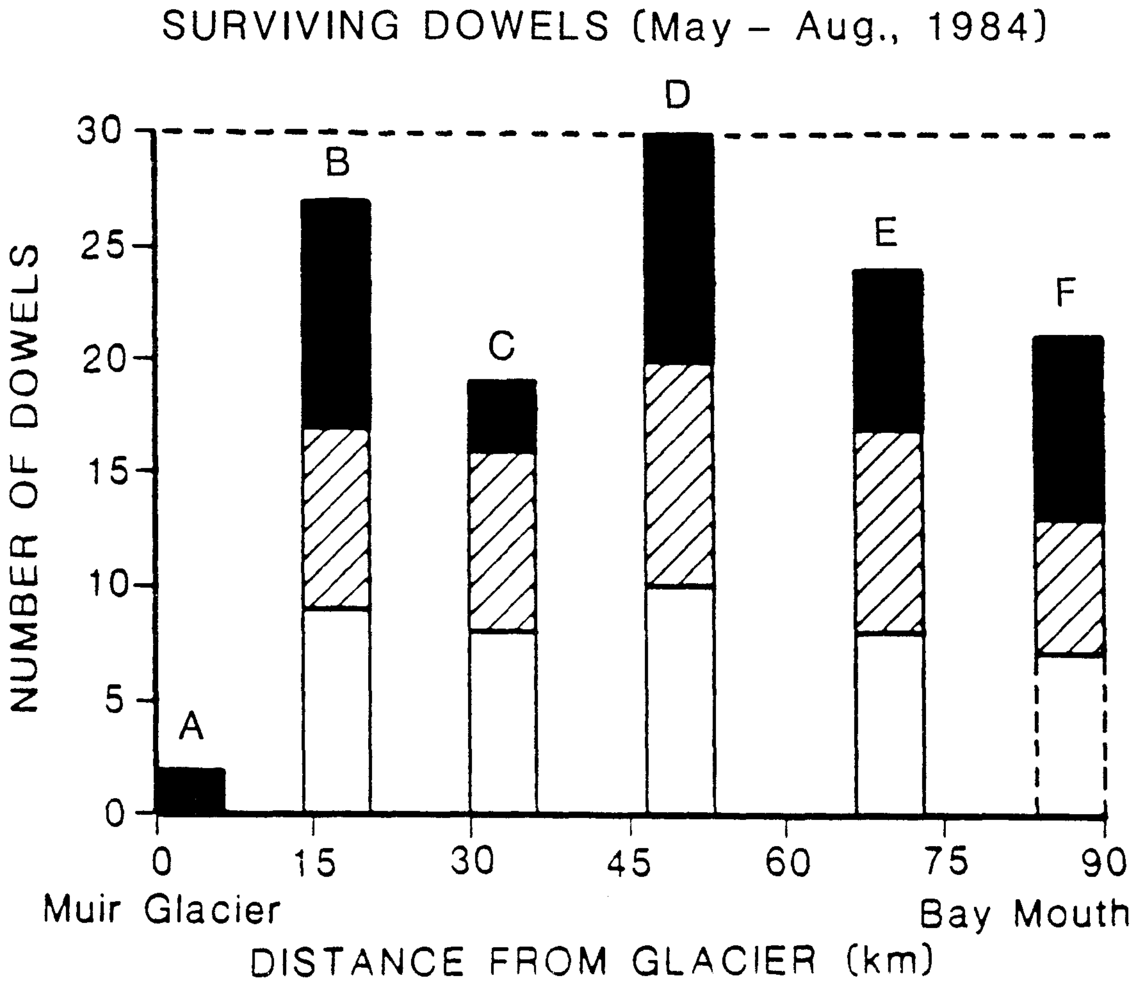


Figure 8. Numbers of dowels remaining attached to boulders after three months. Solid portions represent dowels placed at the 5 m vertical intertidal level; hatched portions represent the 3.5 m level; open portions represent the 2 m level.

would be expected to remain. This was a relatively low number among all six sites, with fewer remaining dowels only at sites A (two remaining) and C (19 remaining). Site F was the most open and exposed to wavewash damage from storms and high winds.

V. Principal components analysis

Principal components analysis (PCA) of the environmental data yielded four eigenvalues that cumulatively explained more than 86% of the total variance in the data (Table 2). The first principal component (PC1), which correlated with amount of total suspended particulates, suspended particulate C and N factors, number of grounded ice fragments, and extinction coefficient, accounted for over 38% of the total variance in the data set. These factors all decreased exponentially with increasing distance from the glacier. An additional 27% was explained by PC2 which represented three more particulate C and N factors (all were parameters that increased linearly with increasing distance from the glacier) and sampling date. PC3 correlated with distance from the glacier, substrate age, water temperature, and salinity; these factors also increased linearly with distance. Finally, PC4 correlated with site aspect, which showed no consistent pattern along the transect.

Of all measured parameters, slope had the lowest correlation coefficient (-0.353 with PC2). Sampling date had the third lowest correlation coefficient > 0.500 (0.821 with PC2). Although it was well correlated with the other factors making up PC2 (suspended particulate N on a weight per volume seawater basis and suspended particulate C and N on a percent weight of total suspended sediment basis), all of which all showed relatively weak linear relationships with distance from the glacier (Figs. 5d, 6a,b), sampling date itself was not significantly correlated with distance (p = 0.38; Fig. 6d).

Air temperature and 1% light depth were not included in the analysis because marine environmental factors were considered most important, and light availability was best described by extinction coefficient.

Biological Community

I. Community composition and vertical zonation

I encountered a total of 54 animal and plant species or species groups (Table 3). Organisms frequently were identified only to the taxonomic level of genus, phylum, or structural group (*e.g.*, dark crustose algal species). Hereafter, "species" will refer to the most discriminating level of identification shown in Table 3 (*e.g.*, I identified members of the Nemertea only to the phylum level, but they will be referred to collectively as a "species"). Consistent patterns of vertical intertidal zonation were apparent. The lowest zone sampled (0 m) included as major species mussels (*Mytilus edulis*), sea stars (*Evasterias troschelii*), urchins (*Strongylocentrotus droebachiensis*), anemones (*Anthopleura elegantissima* and *Tealia crassicornis*), chitons (*Katharina tunicata* and *Tonicella lineata*), and sponges (*Halichondria*

Table 3. List of intertidal species and species groups encountered. Abbreviations are used in Appendices VI and X. "*" denotes the group of limpet species dominated by *Collisella pelta* and also including *C. digitalis*, *Notoacmaea persona*, *N. scutum*, and *Acmaea testudinalis*. "+" denotes the group of barnacle species including *Balanus balanoides*, *B. glandula*, *B. cariosus*, and *B. crenatus*.

Table 3.

Species	Abbreviation
PORIFERA	
Halichondria spp.	Hasp
Haliclona spp.	Hcsp
CNIDARIA	
Anthopleura elegantissima	Anel
Tealia crassicornis	Tecr
NEMERTEA spp.	Nesp
BRYOZOA spp.	Brsp
MOLLUSCA - AMPHINEURA	
Katharina tunicata	Katu
Tonicella lineata	Toli
MOLLUSCA - BIVALVIA	
Mytilus edulis	Myed
Hiatella arctica	Hiar
MOLLUSCA - GASTROPODA	
Collisella spp.*	Cosp
Notoacmaea persona	Nope
Littorina sitkana	Lisi
Thais lima	Thli
Thais lima eggs	Theg
Buccinum baeri	Buba
Margarites pupillus	Mapu
Bittium eschrichtii	Bies
Onchidella borealis	Onbo
ANNELIDA - POLYCHAETA	
Serpula vermicularis	Seve
Spirorbis borealis	Spbo
ECHINODERMATA	
Evasterias troschelii	Evtr
Strongylocentrotus droebachiensis	Stdr

Table 3 (cont.).

Species	Abbreviation
ARTHROPODA - CRUSTACEA	
Balanus spp.†	Basp
Balanus spp. spat†	Bast
Amphipoda spp.	Amsp
Gnorimosphaeroma oregonense	Gnor
Idotea resecata	Idre
Idotea wosnesenskii	Idwo
Pagurus spp.	Pasp
CHORDATA - PISCES	
Anoplarchus purpurescens	Anpu
Gobiesox maeandricus	Goma
Oligocottus maculosus	Olma
CHLOROPHYTA	
Acrosiphonia spp.	Acsp
Ulvales spp.	Ulsp
Urospora/Ulothrix spp.	Uusp
Enteromorpha spp.	Ensp
Green algal slime coating (includes Bacillariophyta)	Grsl
PHAEOPHYTA	
Fucus distichus	Fudi
Soranthera ulvoidea	Soul
Melanosiphon intestinalis	Mein
Laminaria spp.	Lasp
Alaria tenuifolia	Alte
Brown filamentous algal spp.	Brfi
Brown algal slime coating (includes Bacillariophyta)	Brsl
RHODOPHYTA	
Porphyra spp.	Posp
Rhodomela larix	Rhla
Polysiphonia/Pterosiphonia spp.	Ppsp
Halosaccion americanum	Haam
Rhodymenia spp.	Rhsp
Iridaea spp.	Irsp
Gigartina spp.	Gisp
Dark crustose algal spp.	Crsp
Lithothamnium spp.	Lisp

spp. and *Haliclona* spp.). These extended up to the 1.25 m sampling level where other species assumed importance. The algae *Acrosiphonia* spp. and *Rhodomela larix* reached peak percent coverage at this level, and ribbon worms (Nemertea spp.), limpets (*Collisella* spp.), and predatory dogwinkle snails (*Thais lima*) became important (the more recent generic name for *Thais* is *Nucella*). Nemerteans, *Collisella* spp., and *T. lima* remained abundant up to the mid-intertidal 2.5 m level along with *M. edulis*. At 2.5 m, littorine snails (*Littorina sitkana*) and barnacles (*Balanus* spp.) became dominant along with the common rockweed alga *Fucus distichus*. These species extended through the upper intertidal 3.75 m zone where *Notoacmaea persona* became a relatively important limpet grazer. These patterns of vertical zonation were similar to those described at Port Valdez (Keiser 1978; Feder and Keiser 1980), Berners Bay (Calvin 1977), Boca de Quadra (Cimberg 1982), and the protected Washington coast (Suchanek 1978).

II. Species richness patterns

Aspects of the intertidal biological community exhibited clear distance- and/or substrate age-related trends. Because distance from Muir Glacier and substrate age were so closely correlated, "distance/age" hereafter will refer to the gradient described by the two factors collectively. Some species occurred along the entire gradient from baymouth to glacier, but others, which were common in the outer bay, gradually disappeared with decreasing distance from the glacier (Fig. 9). Appendix VI contains frequency and coverage/abundance data

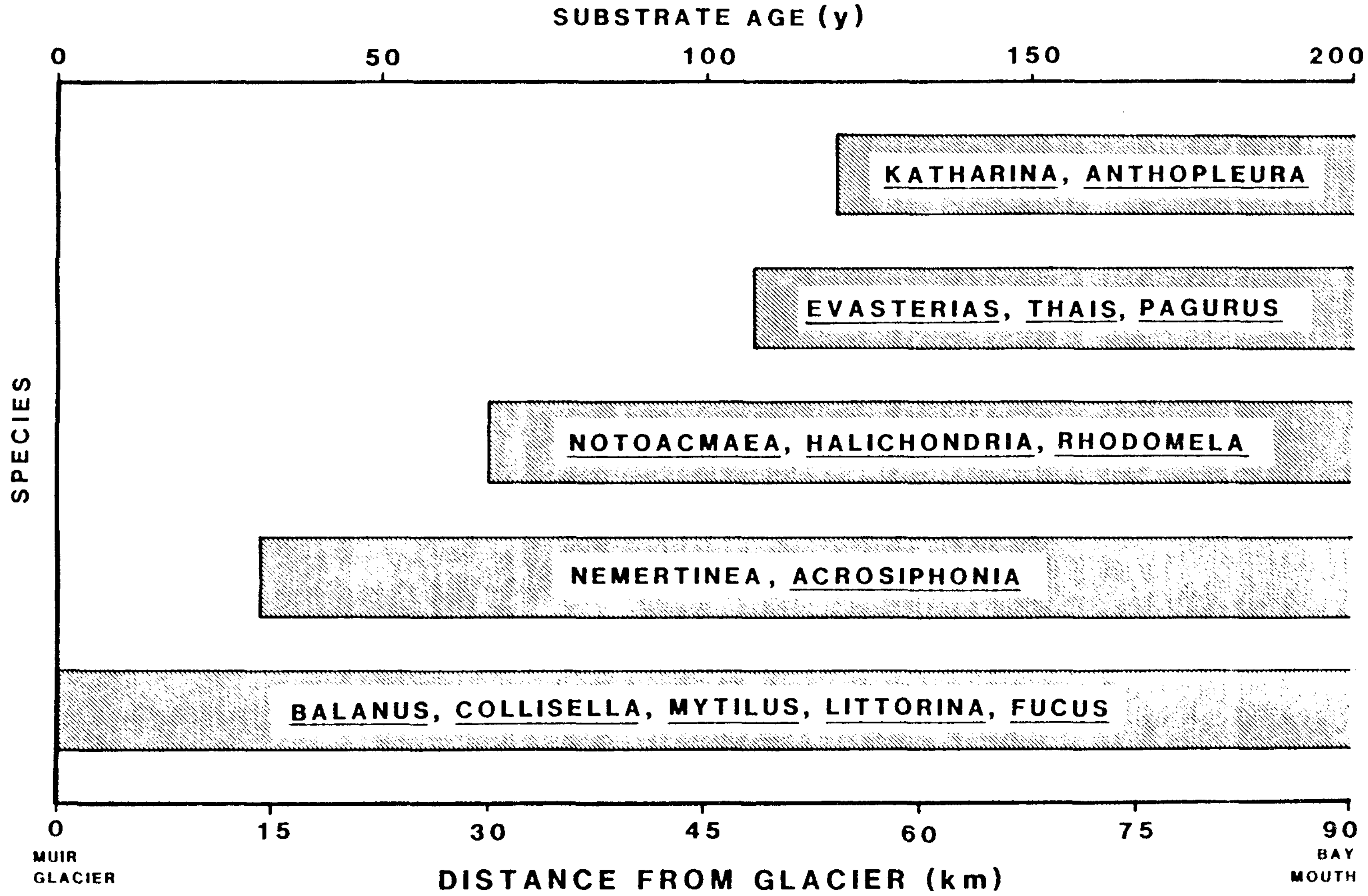


Figure 9. Approximate maximum extents of distribution toward Muir Glacier of major intertidal organisms in Glacier Bay. The more recent name for the phylum Nemertinea is Nemertea.

for all species by site, as well as data for species richness and percent unoccupied surface. Species richness (hereafter defined as the mean number of species encountered per quadrat) increased linearly with increasing distance from the glacier and substrate age at each intertidal level (Fig. 10). Species richness increased more rapidly (based on regression slopes) at the lower intertidal levels (0 and 1.25 m) than at higher levels. In general, the 1.25 m intertidal level was richest in mean number of species; species richness tended to decrease at succeedingly higher intertidal levels. Approximate ranges of species richness for the intertidal levels sampled were 2 to 11 (0 m), 3 to 14 (1.25 m), 2 to 8 (2.5 m), 1 to 7 (3.75 m), and 0 to 4 (5 m). For all levels combined, mean species richness increased with distance/age, ranging from approximately 2 to 8 species (Fig. 11; Appendix VII).

III. Unoccupied surface

In contrast to species richness, percent total unoccupied substrate surface generally exhibited no consistent linear distance/age-related trend. Unoccupied space was not significantly correlated with distance/age at the 0 and 1.25 m intertidal levels (Figs. 12a,b). At the 2.5 and 3.75 m levels there was a curvilinear relationship, with values generally decreasing from approximately 80% near the glacier to a minimum of approximately 5% at 45 km (100 y old) and then increasing again toward the mouth of the bay (Figs. 12c,d). At the 5 m level, percent unoccupied surface decreased linearly with increasing distance/age (Fig. 12e). Not surprisingly, this highest level, which is

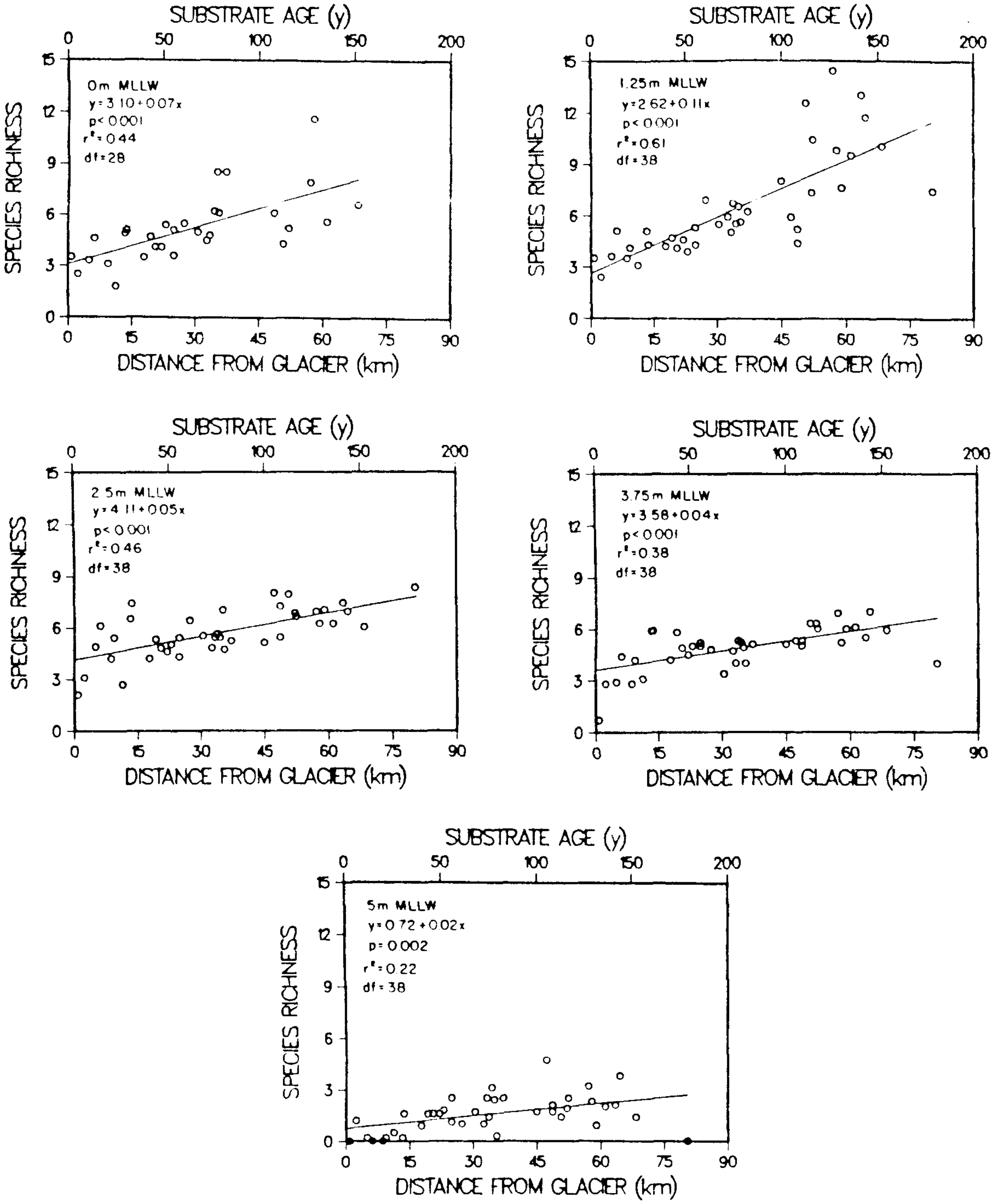


Figure 10. Relationships of intertidal species richness (mean number of species per quadrat) to distance from Muir Glacier and substrate age at five vertical intertidal levels. n = 40 sites except at 0 m where n = 30 sites.

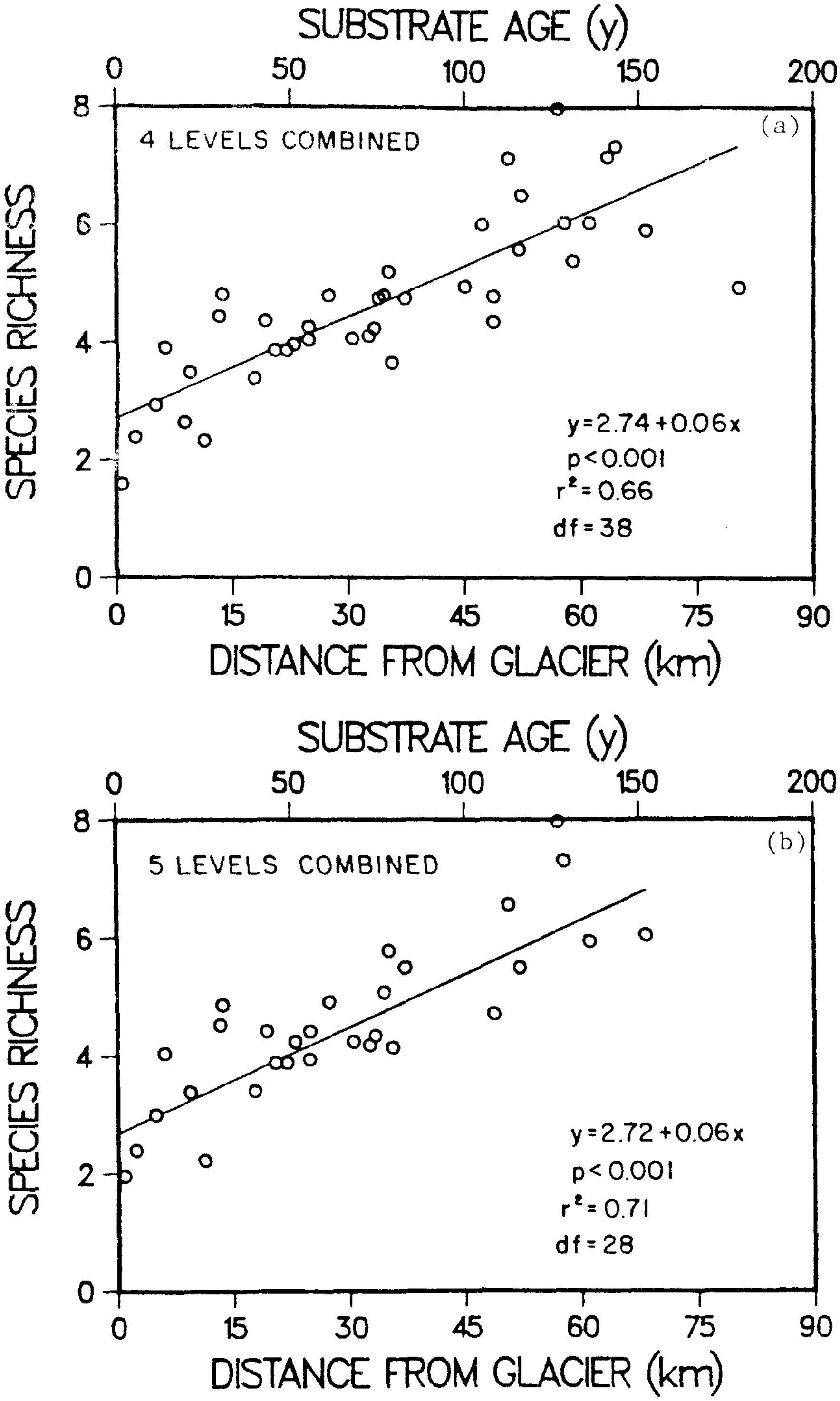


Figure 11. Relationships of intertidal species richness (mean number of species per quadrat) to distance from Muir Glacier and substrate age: (a) four vertical intertidal levels pooled, 1.25 m through 5 m MLLW, n = 40 sites; (b) five levels pooled, 0 m through 5 m MLLW, n = 30 sites.

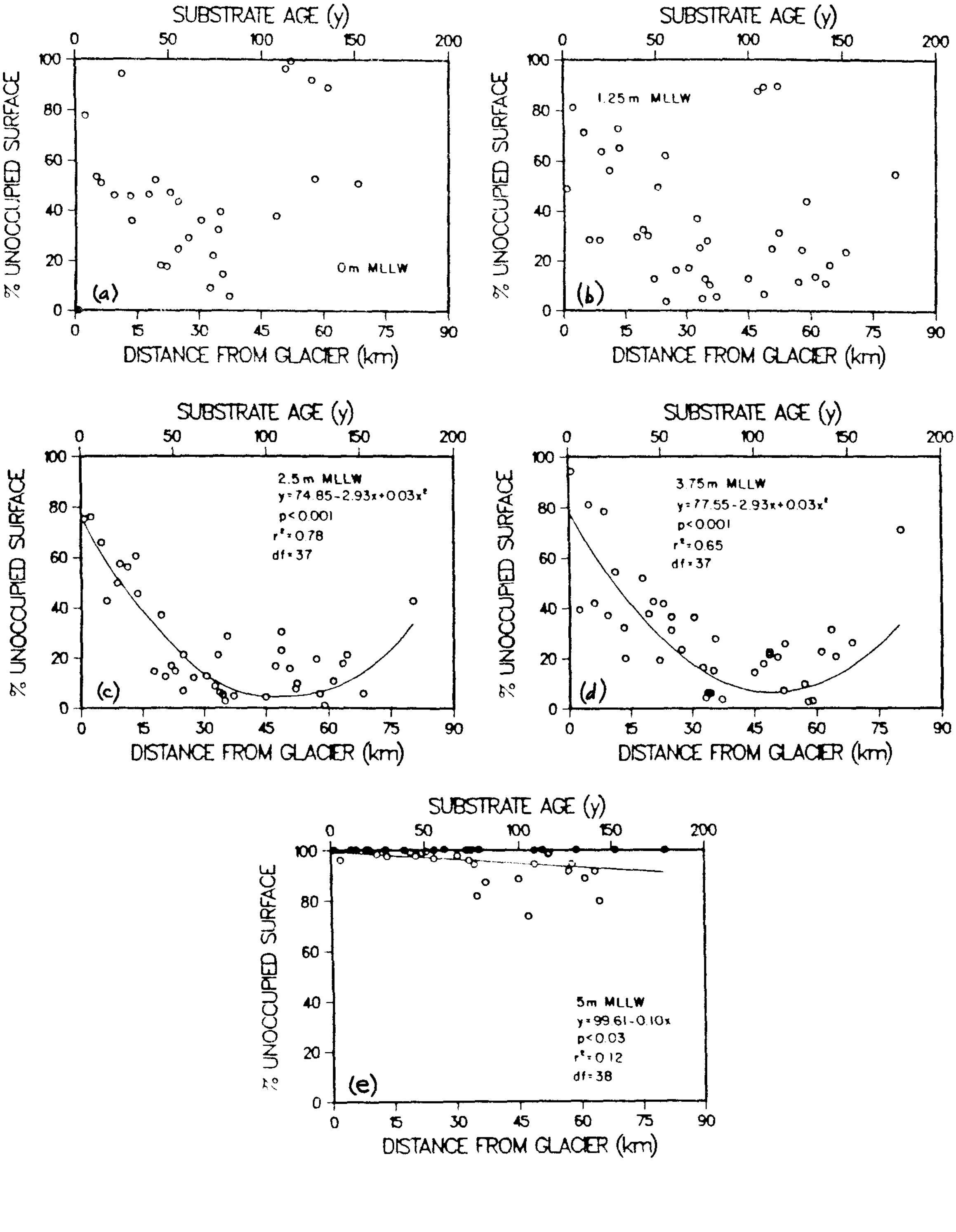


Figure 12. Relationships of unoccupied intertidal substrate surface (mean %) to distance from Muir Glacier and substrate age at five vertical intertidal levels. n = 40 sites except at 0 m where n = 30 sites. Relationships in (a) and (b) are nonsignificant at α = 0.05.

at the extreme intertidal/terrestrial interface, consistently had the greatest proportion of unoccupied space among all levels sampled. No vertical height-related pattern was evident among the four lower levels.

For all intertidal levels combined, percent unoccupied surface exhibited a curvilinear relationship to increasing distance/age (Fig. 13; Appendix VIII). The trend was from approximately 80% near the glacier, decreasing to approximately 35% at 45 km, and increasing again to possibly 60% at the baymouth. The high proportion of unoccupied space close to the glacier was correlated with number of grounded ice fragments (r = 0.64 at 3.75 m; Table 1).

Proportion of intertidal surface covered by ≧ 0.5 cm glacial silt (a component of percent unoccupied surface) decreased exponentially with increasing distance/age (Fig. 14). Silt accumulated to greater degrees on successively lower intertidal surfaces, presumably because of the greater proportion of time these levels were submerged and collecting suspended sediment settling out of the water column. Maximum values for different intertidal levels at sites very close to the glacier were 15% (0 m), 11% (1.25 m), 5% (2.5 m), and 3% (3.75 m). Silt coverage decreased to 0% within 35 to 45 km from the glacier. No silt was encountered on intertidal surfaces at the 5 m level. For all intertidal levels combined, silt coverage decreased exponentially from 2 to 3% close to the glacier, to 0% at approximately 50 km (Fig. 15; Appendix IX).

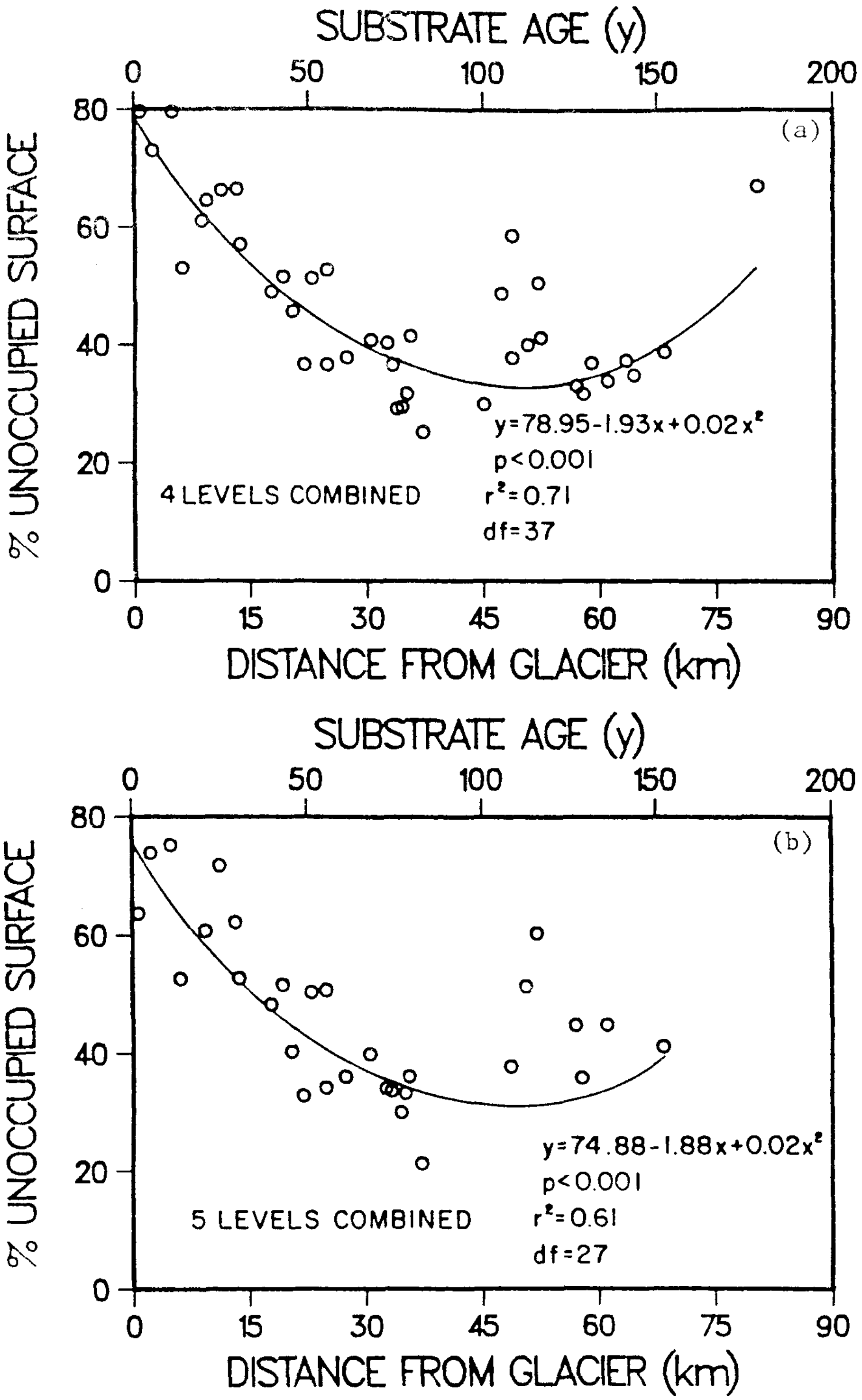


Figure 13. Relationships of unoccupied intertidal substrate surface (mean %) to distance from Muir Glacier and substrate age: (a) four vertical intertidal levels pooled, 1.25 m through 5 m MLLW, n = 40 sites; (b) five levels pooled, 0 m through 5 m MLLW, n = 30 sites.

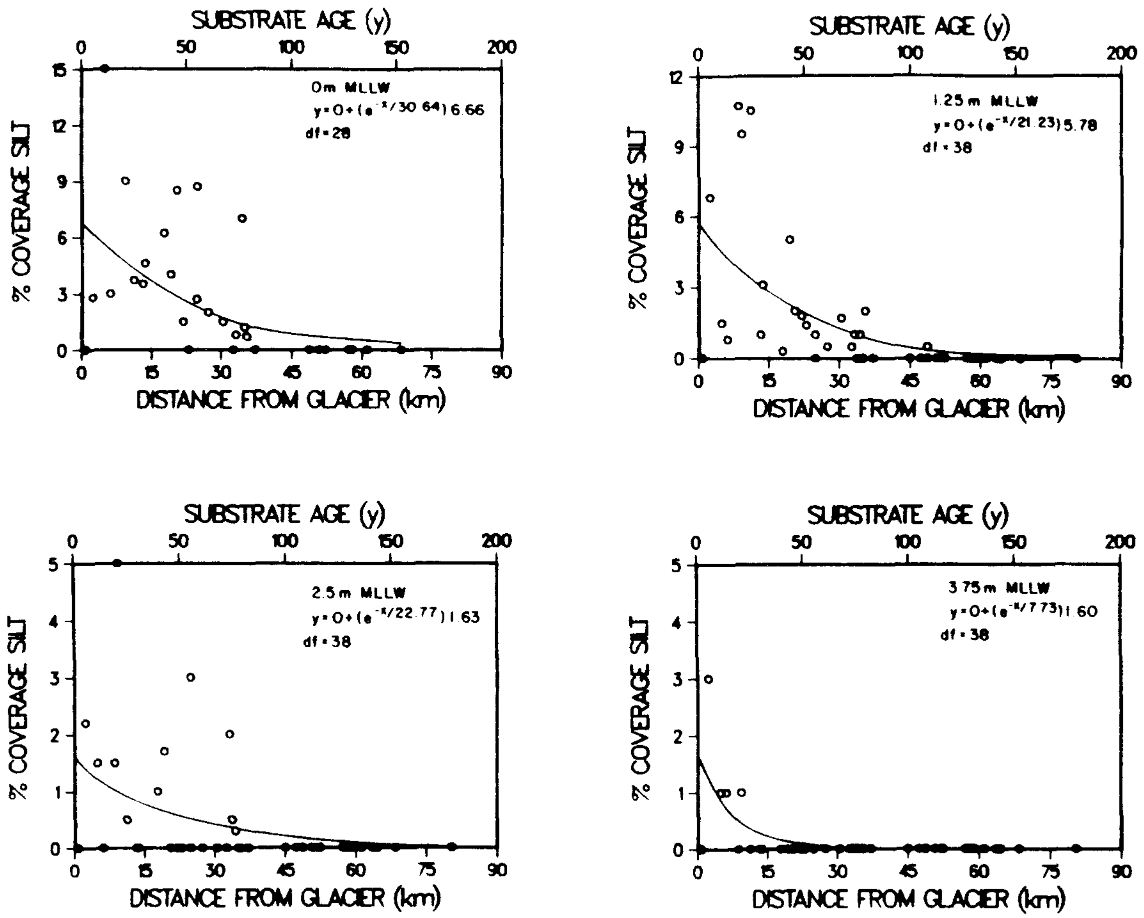
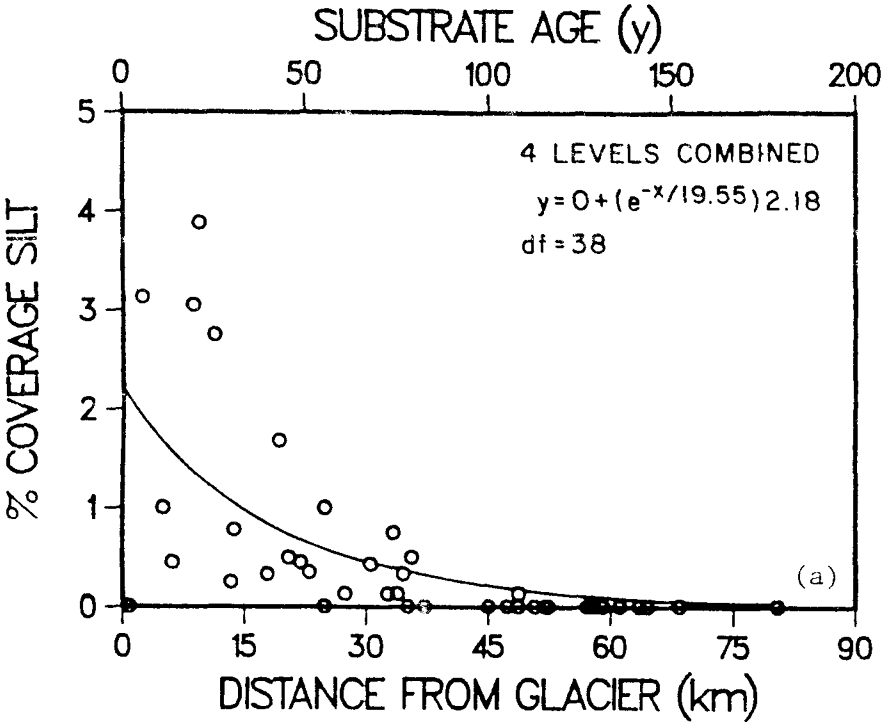


Figure 14. Relationships of intertidal substrate surface covered by ≥ 0.5 cm glacial silt (mean %) to distance from Muir Glacier and substrate age at four vertical intertidal levels. n = 40 sites except at 0 m where n = 30 sites. Silt was absent at the 5 m level.



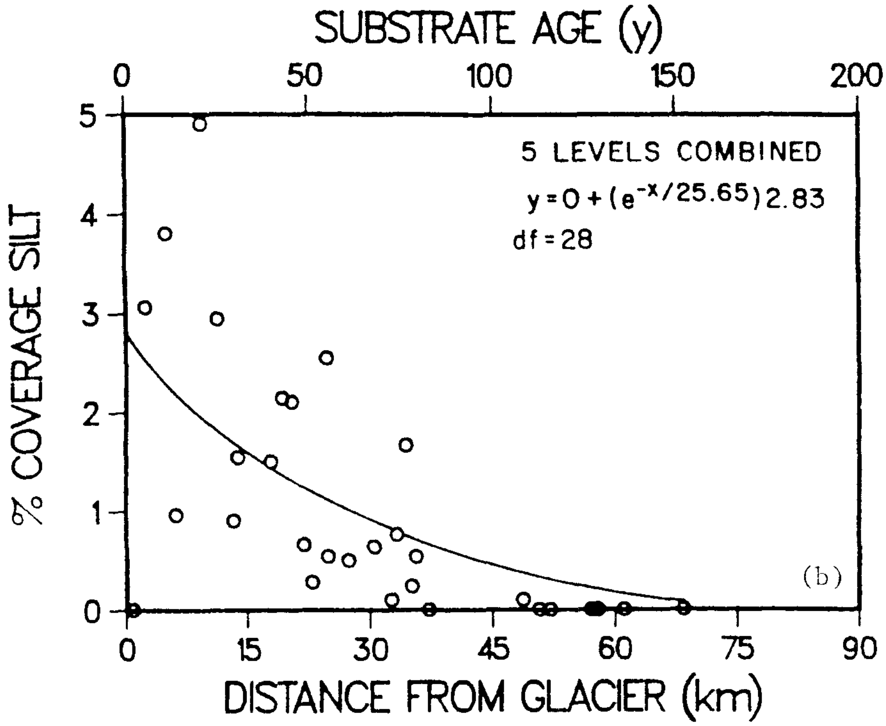


Figure 15. Relationships of intertidal substrate surface covered by ≥ 0.5 cm glacial silt (mean %) to distance from Muir Glacier and substrate age: (a) four vertical intertidal levels pooled, 1.25 m through 5 m MLLW, *n* = 40 sites; (b) five levels pooled, 0 m through 5 m MLLW, *n* = 30 sites.

IV. Principal components analysis

For principal components analysis (PCA) of the biological data, five principal components (PCs) accounted for 48 to 81% of the total variance in species composition at all five intertidal levels, whether frequency or coverage/abundance values were used in the analysis (Table 4). In general, after PC1 (which accounted for 12-35%), each subsequent PC explained approximately 10% more of the total variance. Particularly for the four lowest levels, five PCs consistently explained 48 to 59% of the variance. There was little agreement between results (for a given intertidal level) of frequency analysis and coverage/abundance analysis, however, regarding the grouping of species into "communities" by PC. In addition, species groupings generally were quite different among intertidal levels.

Results of analyses using coverage/abundance data should provide better insights into community composition than those using frequency data, because coverage/abundance data contain more information about the relative distributions of organisms. Using PCA results from the coverage/abundance data, *Halosaccion americanum* and the *Polysiphonia/Pterosiphonia* spp. complex formed an algal group at the 1.25 m (PC1), 2.5 m (PC3), and 3.75 m (PC3) intertidal levels. The only other species pair that formed a group at more than one intertidal level was *Acrosiphonia* spp. and adult *Balanus* spp. at 1.25 m (PC5), 3.75 m (PC5), and 5 m (PC2). *Balanus* spp. adults and *Balanus* spp. juveniles (spat) never formed a group within a single PC in the analysis, nor did *Thais lima* adults and *T. lima* eggs. Adjacent vertical intertidal levels

Tables 4a-e. Results of principal components analysis of intertidal species distributions at five vertical intertidal levels: (a) 0 m MLLW, (b) 1.25 m MLLW, (c) 2.5 m MLLW, (d) 3.75 m MLLW, (e) 5 m MLLW. n = 40 sites except for (a) where n = 30 sites. Left-hand table portions show results computed from frequency data; right-hand table portions show results computed from abundance/coverage data. Any species with a SMC (squared multiple correlation of that species with all other species) of 1.000 (perfectly correlated with all other species) was deleted from the analysis if it occurred less than three times within the 40-site data set. Columns are coefficients of correlation (r) between principal component (PC) and corresponding species. Correlation coefficients with absolute values < .500 have been omitted for clarity. See Table 2 caption for further explanation of values. "*" and "†" denote species groups as described in Table 3 caption. The more recent name for the phylum Nemertinea is Nemertea.

Table 4a. (0 m MLLW)

Species (frequency data)	PC1	PC2	PC3	PC4	PC5
Strongylocentrotus droebachiensis	.941				
Evasterias troschelii	.905				
Mytilus edulis	-.887				
Collisella spp.†	-.601				
Anthopleura elegantissima		.941			
Acrosiphonia spp.		.769	.610		
Littorina sitkana		.724			
Thais lima		.679			
Oligocottus maculosus			.926		
Melanosiphon intestinalis			.754		.526
Margarites pupillus			.595	.562	
Alaria tenuifolia				.921	
Rhodomela larix				.821	
Polysiphonia/Pterosiphonia spp.				.553	
Iridaea spp.					.887
Porphyra spp.					.840
Eigenvalue	5.63	3.87	3.02	2.91	2.36
Total Variance Explained (%)	17.6	12.1	9.4	9.1	7.4
Cumulative Total Variance Explained (%)	17.6	29.7	39.1	48.2	55.6

Species (abundance/ % coverage data)	PC1	PC2	PC3	PC4	PC5
Rhodymenia spp.	.982				
Acrosiphonia spp.	.979				
Thais lima eggs	.959				
Littorina sitkana	.955				
Thais lima	.915				
Hiatella arctica	.832				
Balanus spp. spat*	.779				
Polysiphonia/Pterosiphonia spp.		.984			
Porphyra spp.		.970			
Ulvales		.931			
Alaria tenuifolia		.816			
Oligocottus maculosus			.982		
Margarites pupillus			.962		
Serpula vermicularis			.940		
Lithothamnium spp.			.667		
Strongylocentrotus droebachiensis				.953	
Evasterias troschelii				.864	
Enteromorpha spp.					.978
Brown algal slime coating					.973
Eigenvalue	6.38	4.37	3.93	2.78	2.26
Total Variance Explained (%)	19.3	13.3	11.9	8.4	6.9
Cumulative Total Variance Explained (%)	19.3	32.6	44.5	52.9	59.8

Table 4b. (1.25 m MLLW)

Species (frequency data)	PC1	PC2	PC3	PC4	PC5
Nemertinea	.935				
Katharina tunicata	.907				
Coryanthera ulvoidea	.878				
Evasterias troschelii	.811				
Lithothamnium spp.	.771				
Tealia crassicornis	.759		.521		
Rhodomela larix	.747				
Pagurus spp.	.745				
Mytilus edulis	-.654				
Anoplarchus purpurescens		.855			
Halichondria spp.		.798			
Hiatella arctica	.605	.676			
Thais lima eggs	.579	.661			
Thais lima	.533	.575			
Tonicella lineata			.952		
Halosaccion americanum			.849		
Margarites pupillus			.774		
Melanosiphon intestinalis				.844	
Balanus spp.*				-.755	
Ulvales				.665	
Enteromorpha spp.					.905
Brown algal slime coating					.843
Eigenvalue	11.11	3.51	3.04	2.74	2.40
Total Variance Explained (%)	27.1	8.6	7.4	6.7	5.8
Cumulative Total Variance Explained (%)	27.1	35.7	43.1	49.8	55.6

Species (abundance/ % coverage data)	PC1	PC2	PC3	PC4	PC5
Tonicella lineata	.986				
Lithothamnium spp.	.973				
Balanus spp. spat*	.962				
Tealia crassicornis	.901				
Margarites pupillus	.844				
Halosaccion americanum	.738				
Polysiphonia/Pterosiphonia spp.	.715				
Pagurus spp.	.694	.624			
Ulvales	.587				
Bryozoa		.987			
Nemertinea		.942			
Rhodomela larix		.863			
Evasterias troschelii		.677		.511	
Collisella spp.†		.637			
Thais lima		.623			
Anoplarchus purpurescens			.991		
Halichondria spp.			.932		
Hiatella arctica			.932		
Thais lima eggs			.799		
Melanosiphon intestinalis				.984	
Gigartina spp.				.980	
Katharina tunicata		.621		.769	
Rhodymenia spp.					.974
Acrosiphonia spp.					.829
Balanus spp.*					.512
Eigenvalue	9.35	4.92	3.89	2.96	2.60
Total Variance Explained (%)	22.3	11.7	9.2	7.1	6.2
Cumulative Total Variance Explained (%)	22.3	34.0	43.2	50.3	56.5

Table 4c. (2.5 m MLLW)

Species (frequency data)	PC1	PC2	PC3	PC4	PC5
Tealia crassicornis	.992				
Pagurus spp.	.898				
Halosaccion americanum	.804				
Brown algal slime coating		-.915			
Balanus spp. spat*		.729			
Balanus spp.*	-.553	.714			
Fucus distichus		.636			
Rhodomela larix			.820		
Halichondria spp.			.819		
Soranthera ulvoidea			.805		
Collisella spp.†				.856	
Urospora/Ulothrix spp.				-.769	
Littorina sitkana				.697	
Mytilus edulis		.571		.686	
Oligocottus maculosus					.949
Idotea wosnesenskii					.816
Nemertinea					.787
Lithothamnium spp.					.626
Eigenvalue	5.75	3.65	3.12	2.87	2.41
Total Variance Explained (%)	16.9	10.8	9.1	8.5	7.1
Cumulative Total Variance Explained (%)	16.9	27.7	36.8	45.3	52.4

Species (abundance/ % coverage data)	PC1	PC2	PC3	PC4	PC5
Onchidella borealis	.925				
Thais lima eggs	.920				
Acrosiphonia spp.	.791				
Nemertinea	.730			.571	
Notoacmaea persona		.991			
Dark crustose algal spp.		.991			
Gigartina spp.		.986			
Balanus spp. spat*		.548			.518
Halosaccion americanum			.967		
Lithothamnium spp.			.966		
Polysiphonia/Pterosiphonia spp.			.953		
Oligocottus maculosus				.950	
Idotea wosnesenskii				.831	
Fucus distichus				.791	
Pagurus spp.					.819
Tealia crassicornis					.782
Collisella spp.†					.504
Eigenvalue	4.50	3.54	3.46	2.96	2.47
Total Variance Explained (%)	12.9	10.1	9.9	8.4	7.1
Cumulative Total Variance Explained (%)	12.9	23.0	32.9	41.3	48.4

Table 4d. (3.75 m MLLW)

Species (frequency data)	PC1	PC2	PC3	PC4	PC5
Mytilus edulis	.876				
Balanus spp. spat*	.852				
Collisella spp.†	.844				
Littorina sitkana	.735				
Fucus distichus	.661				
Balanus spp.*	.581			.527	
Dark crustose algal spp.		.933			
Pagurus spp.		.882			
Rhodomela larix		.702			
Thais lima		.651			
Amphipoda			.863		
Gnorimosphaeroma oregonense			.846		
Brown filamentous algal spp.			.806		
Halosaccion americanum				.935	
Polysiphonia/Pterosiphonia spp.				.893	
Ulvales					.906
Idotea wosnesenskii					.876
Eigenvalue	5.19	3.06	2.41	1.96	1.82
Total Variance Explained (%)	19.2	11.3	9.0	7.2	6.8
Cumulative Total Variance Explained (%)	19.2	30.5	39.5	46.7	53.5

Species (abundance/ % coverage data)	PC1	PC2	PC3	PC4	PC5
Brown filamentous algal spp.	.951				
Gnorimosphaeroma oregonense	.930				
Amphipoda	.885				
Rhodomela larix		.864			
Dark crustose algal spp.		.843			
Thais lima		.745			
Collisella spp.†		.599			
Halosaccion americanum			.959		
Polysiphonia/Pterosiphonia spp.			.931		
Balanus spp. spat*			.674		
Melanosiphon intestinalis				.916	
Notoacmaea persona				.872	
Fucus distichus				.525	
Littorina sitkana					.815
Balanus spp.*					.769
Urospora/Ulothrix spp.					-.532
Acrosiphonia spp.					.516
Eigenvalue	3.58	3.03	2.35	2.00	1.90
Total Variance Explained (%)	13.8	11.7	9.0	7.7	7.3
Cumulative Total Variance Explained (%)	13.8	25.5	34.5	42.2	49.5

Table 4e. (5 m MLLW)

Species (frequency data)	PC1	PC2	PC3	PC4	PC5
Mytilus edulis	.858				
Acrosiphonia spp.	.855				
Notoacmaea persona	.843				
Gigartina spp.		.932			
Collisella spp.†		.865			
Balanus spp. spat*		.757			
Littorina sitkana			.775		
Balanus spp.*			.711		
Urospora/Ulothrix spp.			-.667		
Idotea wosnesenskii				.755	
Enteromorpha spp.				-.646	
Green algal slime coating					.929
Eigenvalue	4.60	1.56	1.42	1.14	1.09
Total Variance Explained (%)	35.4	12.0	10.9	8.8	8.3
Cumulative Total Variance Explained (%)	35.4	47.4	58.3	67.1	75.4

Species (abundance/ % coverage data)	PC1	PC2	PC3	PC4	PC5
Collisella spp.†	.956				
Balanus spp. spat*	.887				
Gigartina spp.	.886				
Fucus distichus	.824				
Notoacmaea persona		.861			
Acrosiphonia spp.		.824			
Mytilus edulis	.558	.783			
Balanus spp.*		.641		.502	
Green algal slime coating			.926		
Enteromorpha spp.			.911		
Littorina sitkana				.832	
Urospora/Ulothrix spp.				-.563	
Idotea wosnesenskii					.860
Eigenvalue	4.64	1.92	1.76	1.18	1.02
Total Variance Explained (%)	35.7	14.8	13.5	9.1	7.9
Cumulative Total Variance Explained (%)	35.7	50.5	64.0	73.1	81.0

shared species pairs comprising one of their PCs (although usually a different PC) more frequently than did non-adjacent intertidal levels. Immediately adjacent levels shared species pairs within individual PCs nine times; levels separated from each other by another level (*e.g.*, 1.25 and 3.75 m) shared species pairs four times; and levels (1.25 and 5 m) separated by two or more intermediate levels shared species pairs only once.

V. Species distribution patterns

Balanus spp. adults and juveniles (spat) reached their greatest coverages at the 2.5 and 3.75 m intertidal levels, respectively (Fig. 16). In general, spat peaked in coverage farther from the glacier than did adults at a given level. At the 0 and 2.5 m levels adults tended to be more successful closer to the glacier than farther away, while in the upper intertidal (3.75-5 m) their greatest coverage was in the middle portion of the bay.

Mytilus edulis was important at all vertical intertidal levels through 3.75 m (Fig. 17). At 0 and 1.25 m it was most successful in the inner half of the bay. At the 2.5 m level and above, peak coverage was in the outer half of the bay.

Evasterias troschelii occurred only up to the 2.5 m vertical intertidal level and was most abundant at 1.25 m (Fig. 17). It was restricted exclusively to sites beyond 45 km from the glacier. This 45-km threshold also was the point where *M. edulis* coverage fell sharply at

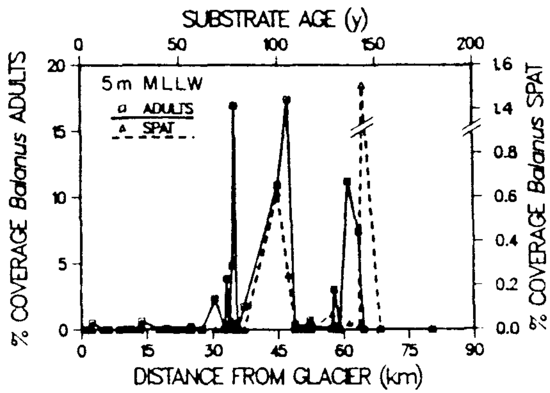
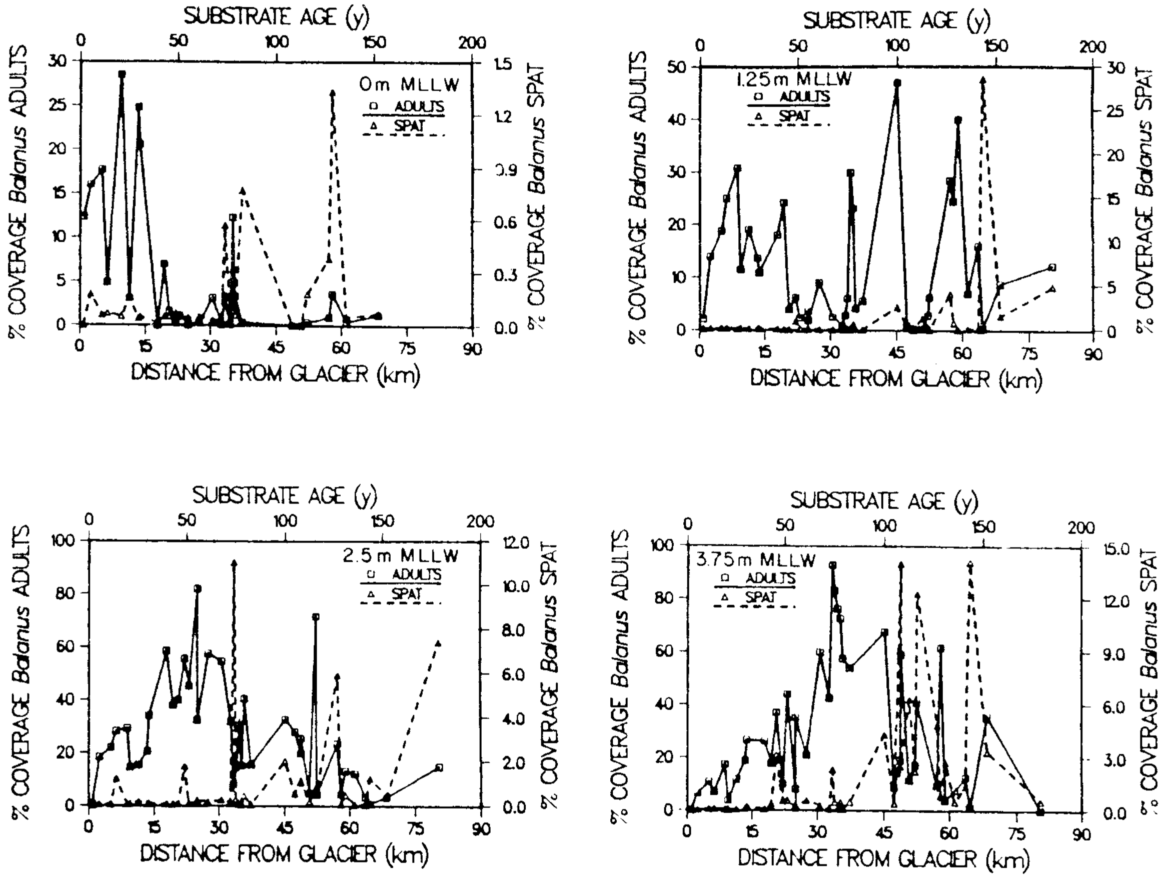


Figure 16. Relationships of cover (mean %) by *Balanus* spp. adults and juveniles (spat) to distance from Muir Glacier and substrate age at five vertical intertidal levels. n = 40 sites except at 0 m where n = 30 sites.



SUBSTRATE AGE (y)
% COVERAGE Balanus ADULTS
% COVERAGE Balanus SPAT
DISTANCE FROM GLACIER (km)
0 m MLLW
ADULTS
SPAT
1.25 m MLLW
2.5 m MLLW
3.75 m MLLW

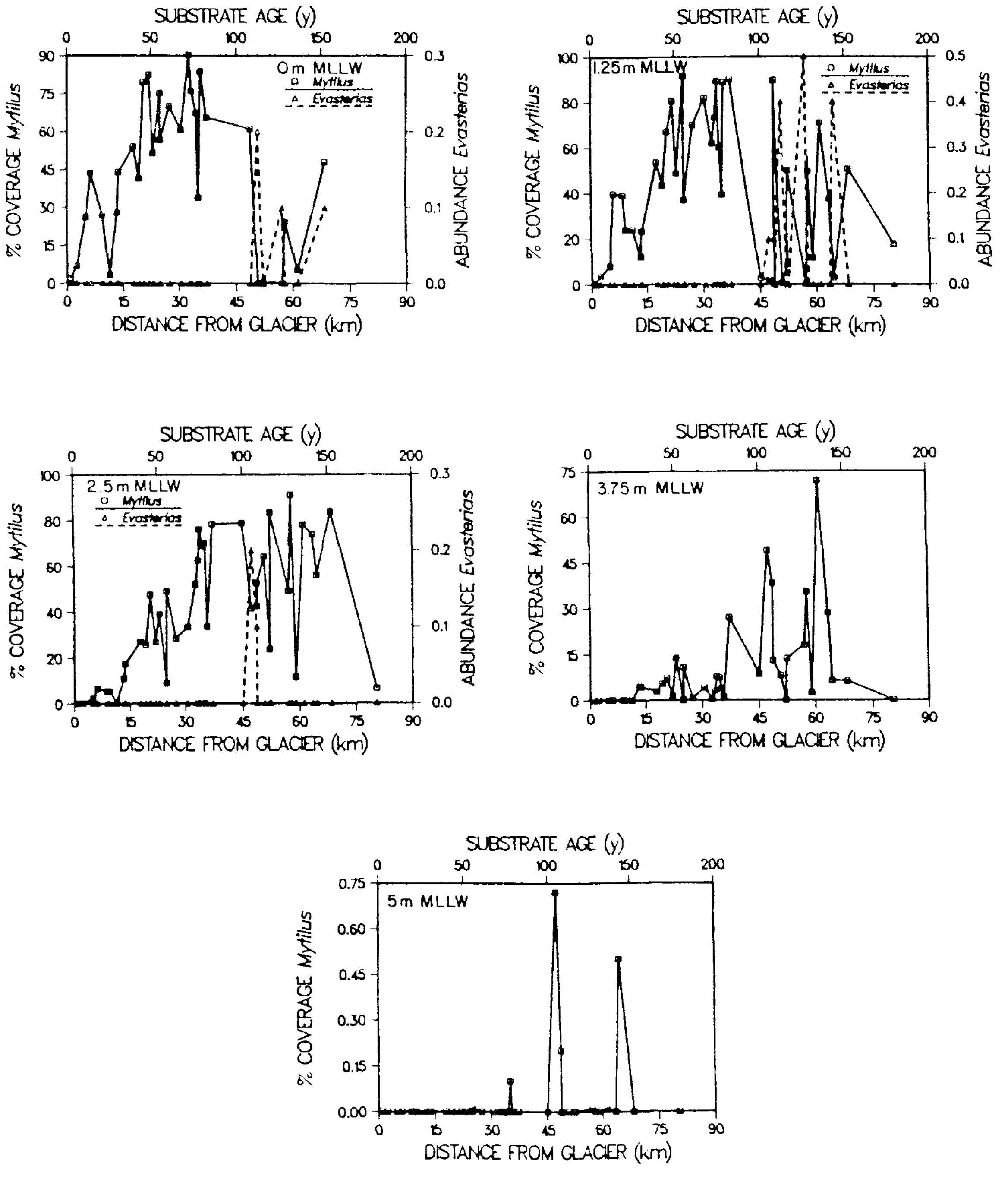


Figure 17. Relationships of cover (mean %) by *Mytilus edulis* and abundance (mean number of individuals per 0.1 m^2) of *Evasterias troschelii* to distance from Muir Glacier and substrate age at five vertical intertidal levels. n = 40 sites except at 0 m where n = 30 sites. *E. troschelii* was absent above 2.5 m.

the lower 0 and 1.25 m vertical intertidal levels. *E. troschelii* is a major predator of *M. edulis* and *Balanus* spp.in Glacier Bay.

Relative abundance patterns of *Thais lima* adults and coverage patterns of *T. lima* eggs were very similar at the 0 through 2.5 m levels where they occurred together (Fig. 18). Like *E. troschelii*, they were most successful at the 1.25 m level, and range was restricted to sites beyond 45 km from the glacier. Eggs were not encountered at vertical levels higher than 2.5 m, and adults were not encountered higher than 3.75 m. *T. lima* is the other major predator of mussels and barnacles in Glacier Bay.

Collisella spp. also reached their maximum abundance in the middle portion of the bay, along with chitons (Fig. 19). *Collisella* spp. were most successful at the 0 through 2.5 m levels, while chitons were restricted to the two lowest levels and did not occur closer than 45 km from the glacier.

Relative abundance patterns of *Littorina sitkana* and coverage patterns of *Fucus distichus* were similar to those of *Collisella* spp., with peaks in the middle portion of the bay at all intertidal levels (Fig. 20). Both species were most successful, along with *Balanus* spp., at the 3.75 m mid- to upper intertidal level. At the lower 0 and 1.25 m levels, *F. distichus* appeared able to persist in greater relative amount close to the glacier (within 15 km) than did *L. sitkana*. Like *Balanus* spp., *F. distichus* at the 0 m level was more successful at sites close to the glacier than at sites farther away from the glacier.

Nemerteans and sponges occurred most frequently at sites in the mid- to outer portions of the bay, especially at the 0 and 1.25 m

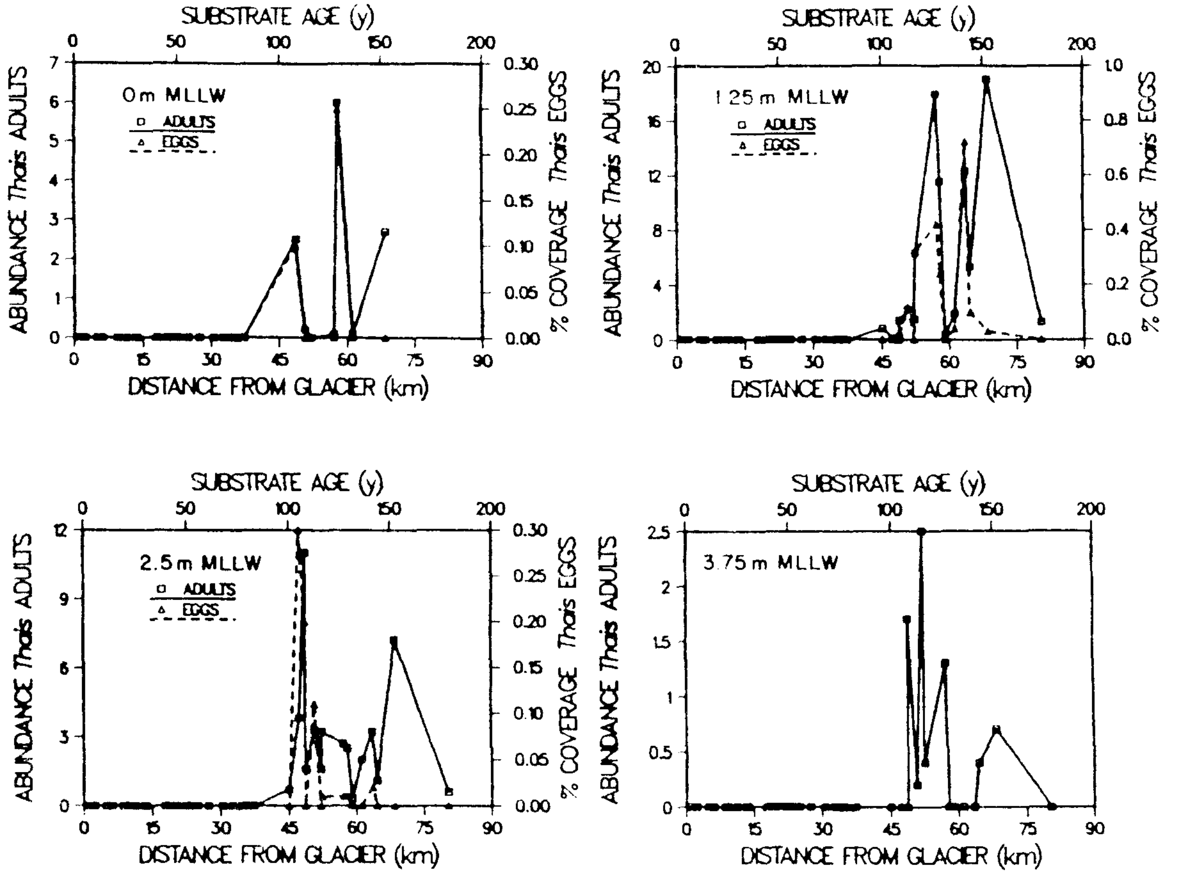


Figure 18. Relationships of abundance (mean number of individuals per 0.1 m^2) of *Thais lima* adults and cover (mean %) by *T. lima* eggs to distance from Muir Glacier and substrate age at four vertical intertidal levels. *n* = 40 sites except at 0 m where n = 30 sites. Adults and eggs were absent above 3.75 and 2.5 m, respectively.

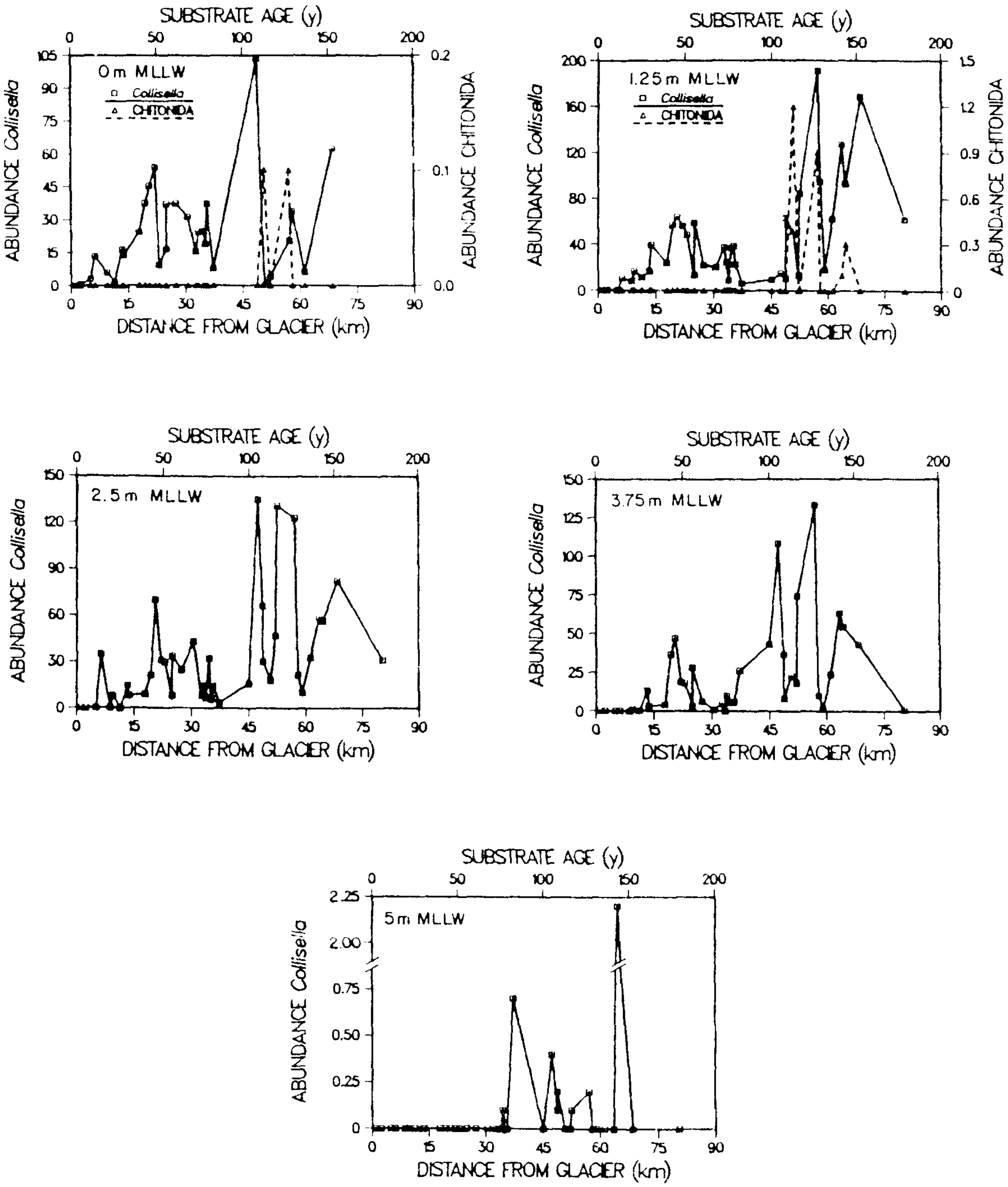


Figure 19. Relationships of abundance (mean number of individuals per 0.1 m^2) of *Collisella* spp. and Chitonida (= Amphineura) spp. to distance from Muir Glacier and substrate age at five vertical intertidal levels. n = 40 sites except at 0 m where *n* = 30 sites. Chitonida spp. were absent above 1.25 m.

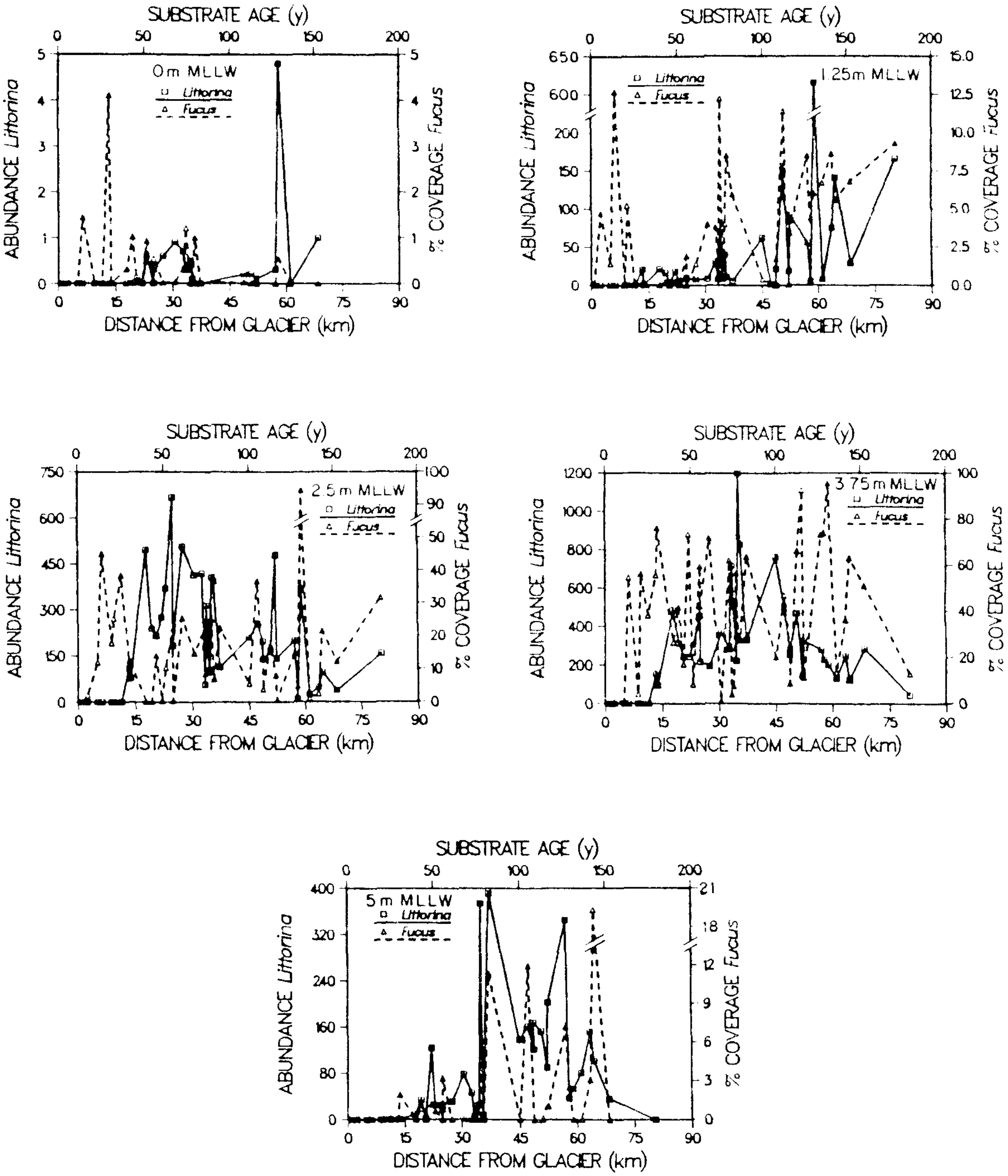


Figure 20. Relationships of abundance (mean number of individuals per 0.1 m^2) of *Littorina sitkana* and cover (mean %) by *Fucus distichus* to distance from Muir Glacier and substrate age at five vertical intertidal levels. $n = 40$ sites except at 0 m where $n = 30$ sites.

intertidal levels (Fig. 21). Nemerteans were not encountered at levels above 3.75 m, nor closer than 15 km from the glacier. Sponges were not encountered at levels above 2.5 m, nor closer than 30 km from the glacier.

Anemones and hermit crabs (*Pagurus* spp.) were restricted to outer bay sites at least 45 km from the glacier, and both appeared to be most successful at the 1.25 m intertidal level (Fig. 22). Neither was encountered higher than 3.75 m.

Acrosiphonia spp. and *Rhodomela larix* exhibited similar patterns of peak coverage in the mid- to outer portions of the bay beyond 30 km from the glacier (Fig. 23). Both were most successful at the 1.25 m intertidal level. *R. larix* was not encountered above 3.75 m.

From these distributional results it is apparent that several species or species groups were severely restricted in their distributions toward the head of the bay at three approximate "threshold" distances (where coverage or abundance dropped sharply or occurrence ceased altogether) from the glacier: 15 km (*L. sitkana* and Nemertea spp.), 30 to 35 km (Porifera spp., *Acrosiphonia* spp., and *R. larix*), and 45 km (*E. troschelii*, *T. lima*, Amphineura spp., Anthozoa spp., and *Pagurus* spp.). There also were "threshold" distances from the glacier where several environmental factors changed rapidly: 10 km (suspended particulate C on weight per volume seawater basis; Fig. 7d), 15 km (total suspended particulates per volume and particulate C:N ratio; Figs. 7a and 7e, respectively), 25 km (light extinction coefficient and number of grounded ice fragments; Figs. 7b and 7c, respectively), and 35 to 45 km (strong near-surface depth-related

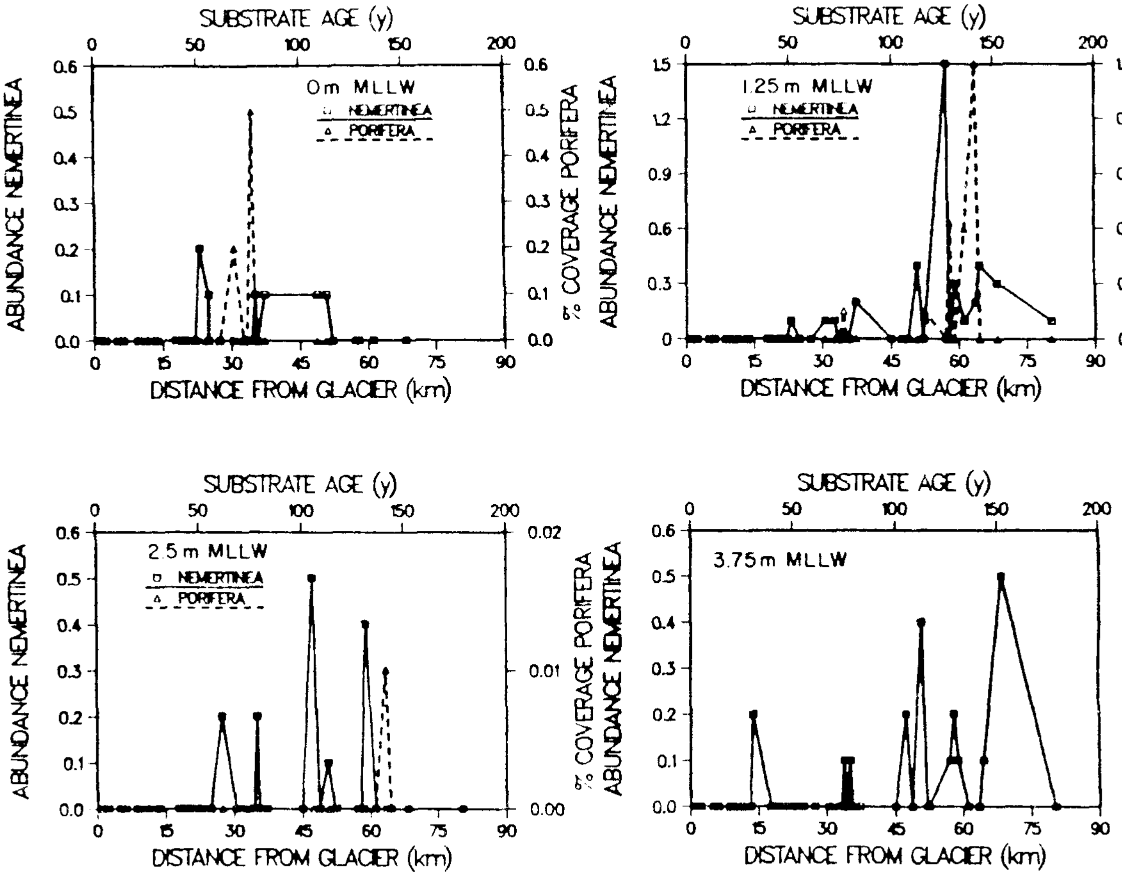


Figure 21. Relationships of abundance (mean number of individuals per 0.1 m^2) of Nemertinea (more recently Nemertea) spp. and cover (mean %) by Porifera spp. to distance from Muir Glacier and substrate age at five vertical intertidal levels. n = 40 sites except at 0 m where n = 30 sites. Porifera spp. and Nemertinea spp. were absent above 2.5 and 3.75 m, respectively.

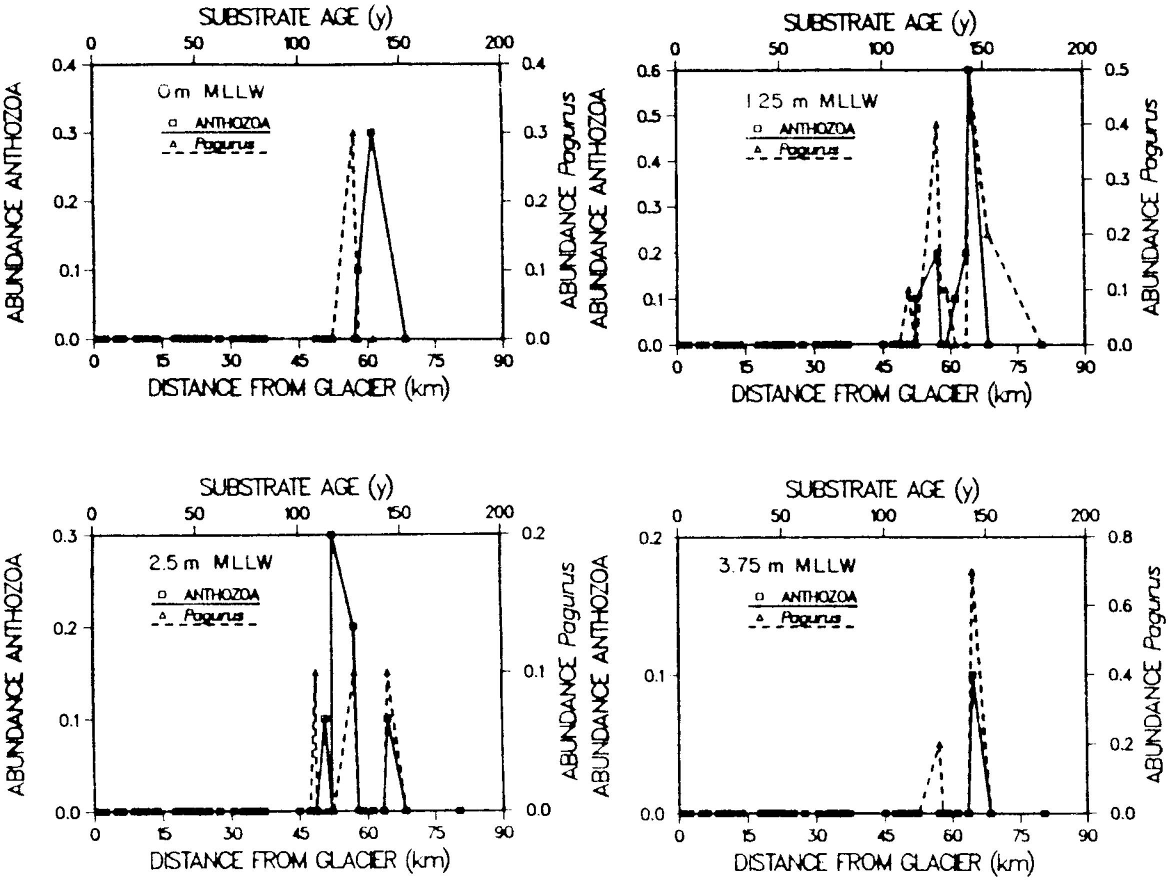


Figure 22. Relationships of abundance (mean number of individuals per 0.1 m^2) of Anthozoa spp. and *Pagurus* spp. to distance from Muir Glacier and substrate age at five vertical intertidal levels. n = 40 sites except at 0 m where n = 30 sites. Both groups were absent above 3.75 m.

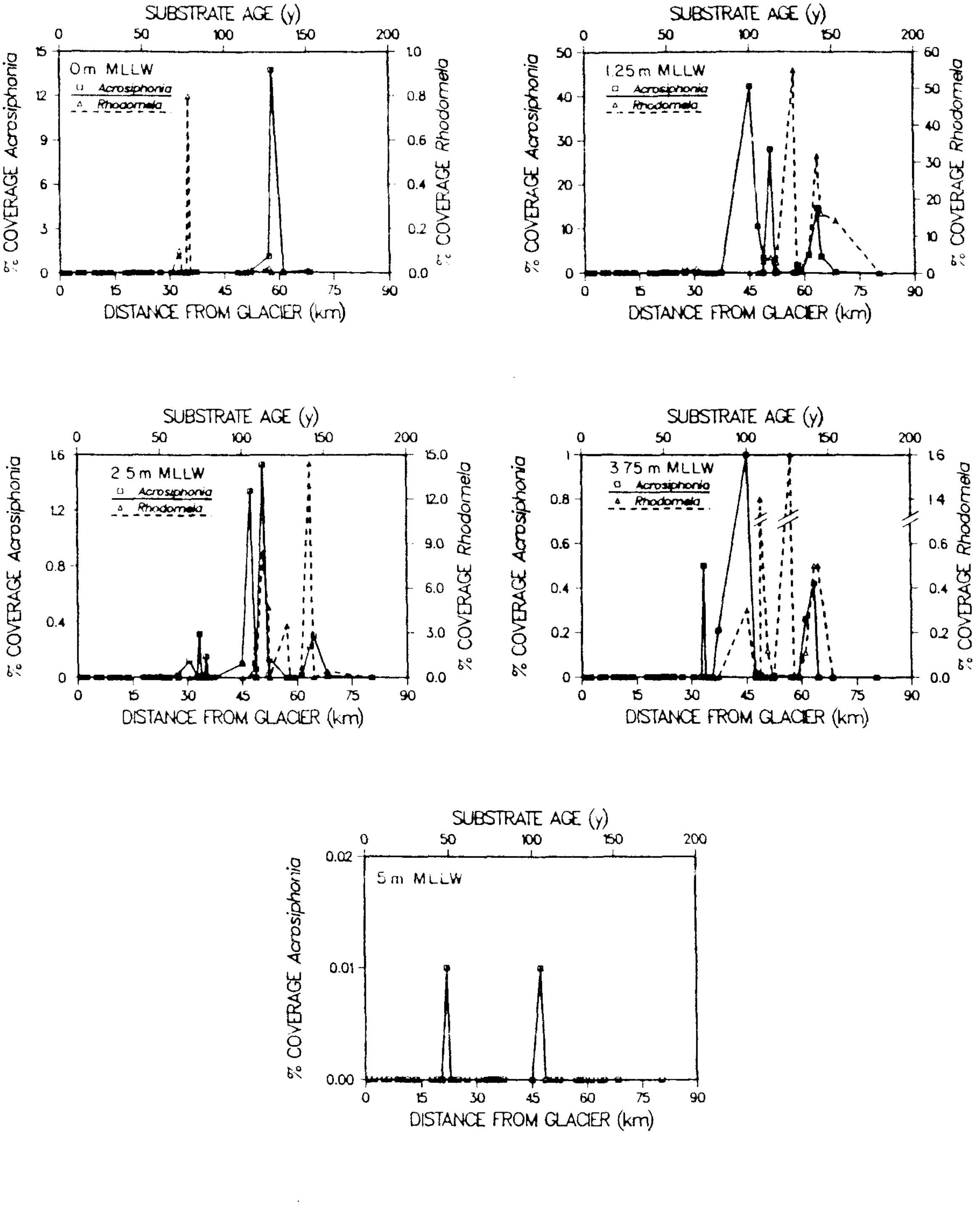


Figure 23. Relationships of cover (mean %) by *Acrosiphonia* spp. and *Rhodomela larix* to distance from Muir Glacier and substrate age at five vertical intertidal levels. *n* = 40 sites except at 0 m where n = 30 sites. *R. larix* was absent above 3.75 m.

salinity increases and percent silt coverage of substrate; Appendix III and Figs. 14 and 15, respectively).

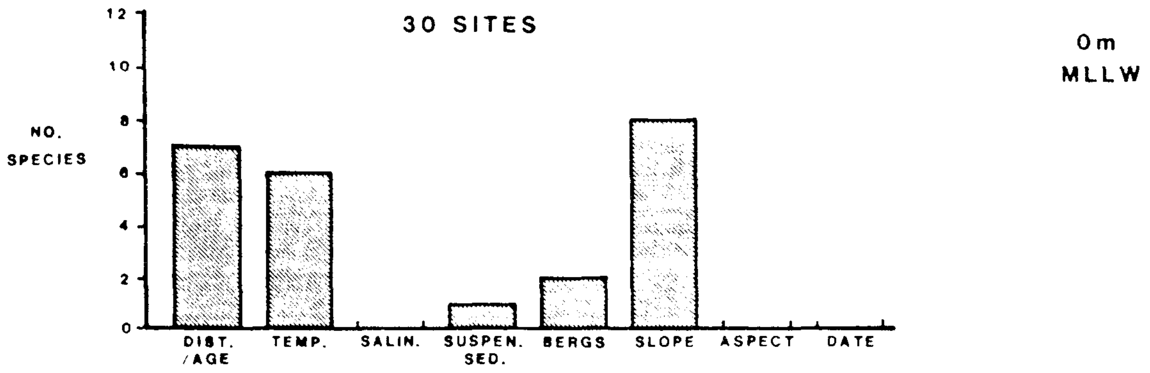
VI. Relative importance of environmental parameters: stepwise multiple regressions and principal components analysis

Stepwise multiple regression analyses for each species (using either percent coverage or abundance) at each intertidal height *vs.* all environmental parameters (except air temperature and 1% light depth) showed that approximately half of the species at each intertidal level were not significantly correlated with any environmental variable in the analysis (critical F = 4.000; Appendix X). When results from all intertidal levels for all 40 sites (Figs. 24a-e) were combined, stepwise multiple regression analyses most frequently identified the distance/age factor and water temperature as the environmental factors that best predicted or statistically "explained" the greatest number of species distributions (Fig. 24f). When particulate C and N data (available for 26 of the 40 sites) were added into the analyses, the distance/age factor remained important; however, suspended particulate N factors and salinity were most strongly correlated with the distributions of species more often than was water temperature (Fig. 24f).

When species richness values were regressed against all environmental factors, the distance/age parameter was the best predictor of species richness at most vertical intertidal levels (Table 5). Near-surface water temperature and total suspended particulates also were important predictors of species richness. Water temperature was

Figures 24a-f.

Results of stepwise multiple regressions of individual species distributions (using coverage/abundance data) against all environmental parameters measured (including sampling date and excluding air temperature and 1% light depth). Column heights represent number of species distributional patterns that were most highly correlated with the corresponding environmental parameter. "Suspen. Sed." includes the sum of species that correlated most strongly with total suspended particulate concentration in seawater and extinction coefficient; "PC" (suspended particulate carbon) and "PN" (suspended particulate nitrogen) categories each include the sum of species that correlated most strongly with those parameters as measured by either concentration in seawater or percent of total suspended particulates by weight; "Bergs" means number of ice fragments. For each figure, the lower histogram shows results from the data set containing PC and PN measurements (n = 26 sites), and the upper histogram shows results from the data set that does not include those measurements (n = 40 sites).



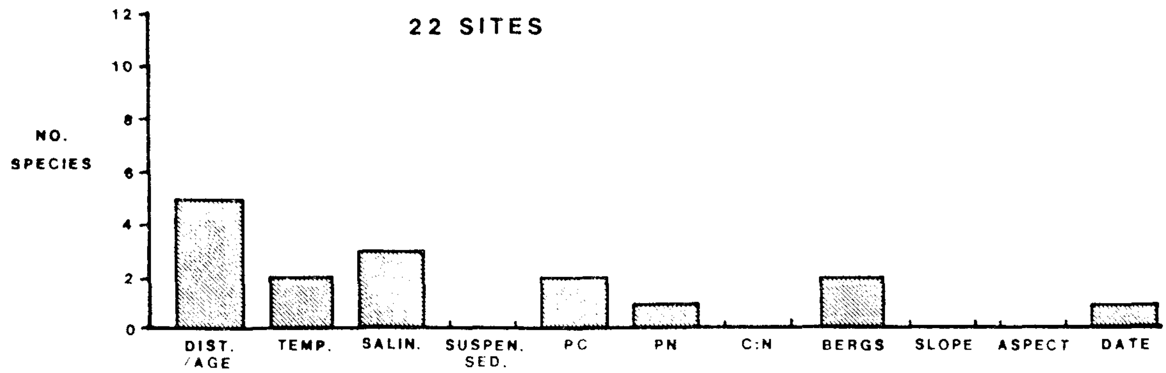


Figure 24a. Results from the 0 m MLLW vertical intertidal level. Results are from smaller data sets (n = 22 and 30 sites) than those at higher levels because biological data at 0 m were collected from 30 of the 40 sites.

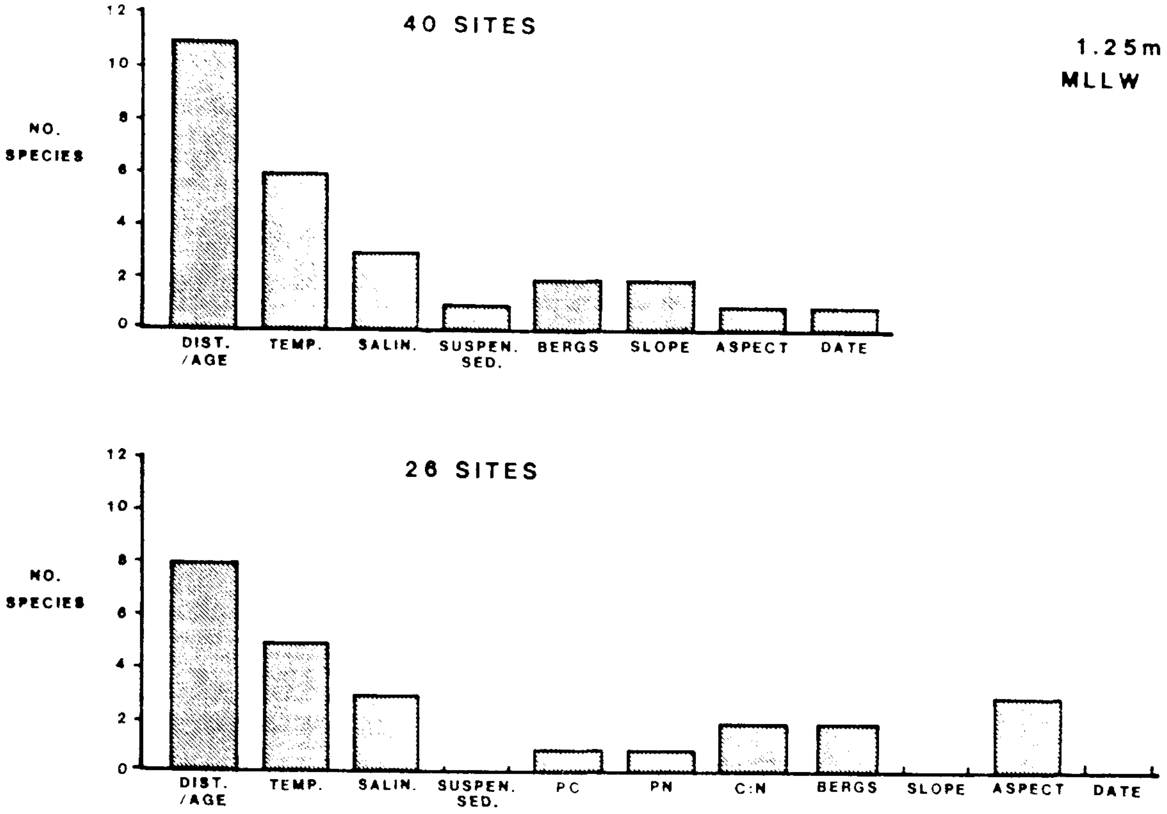


Figure 24b. Results from the 1.25 m MLLW vertical intertidal level.

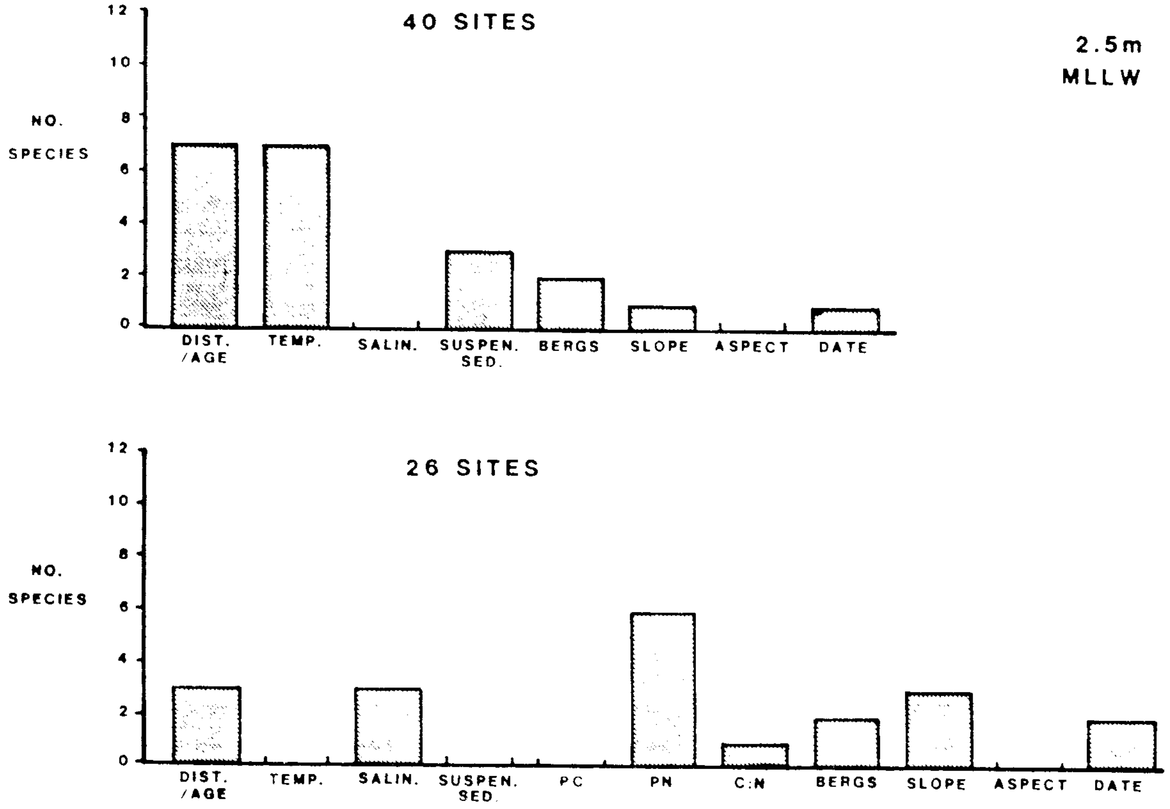


Figure 24c. Results from the 2.5 m MLLW vertical intertidal level.

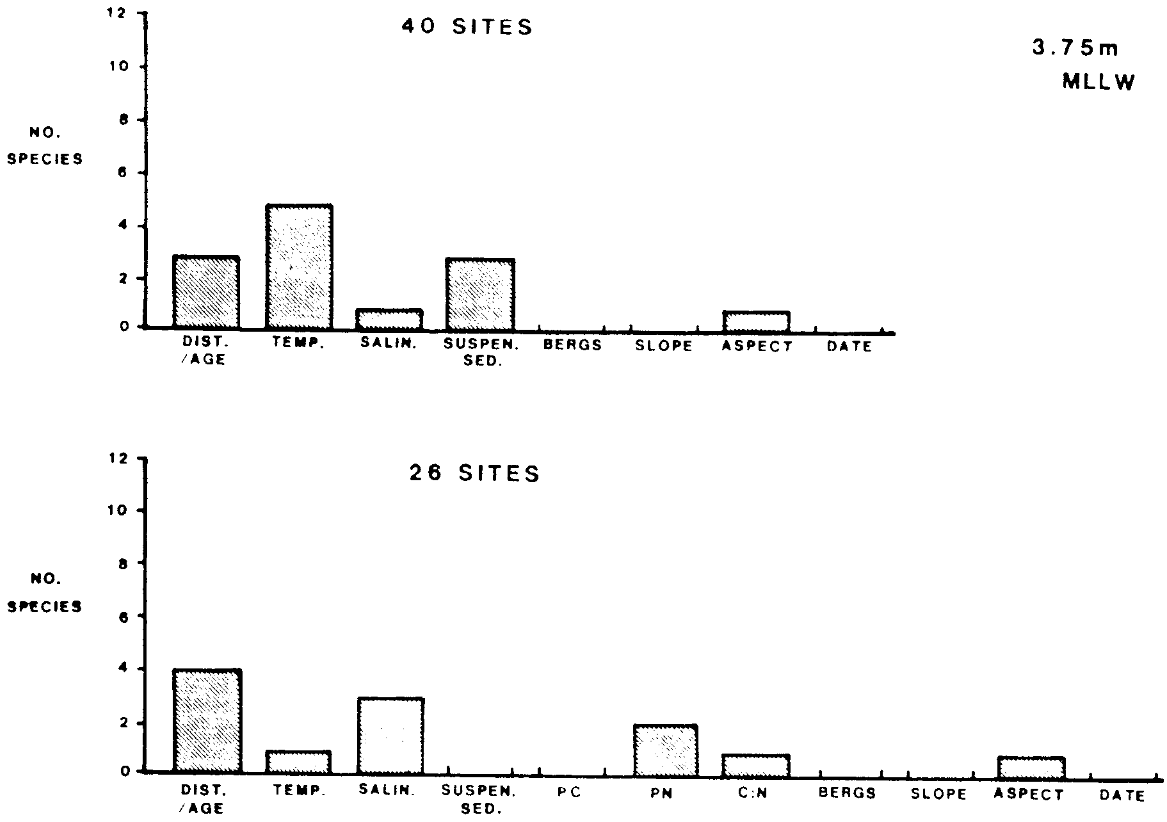


Figure 24d. Results from the 3.75 m MLLW vertical intertidal level.

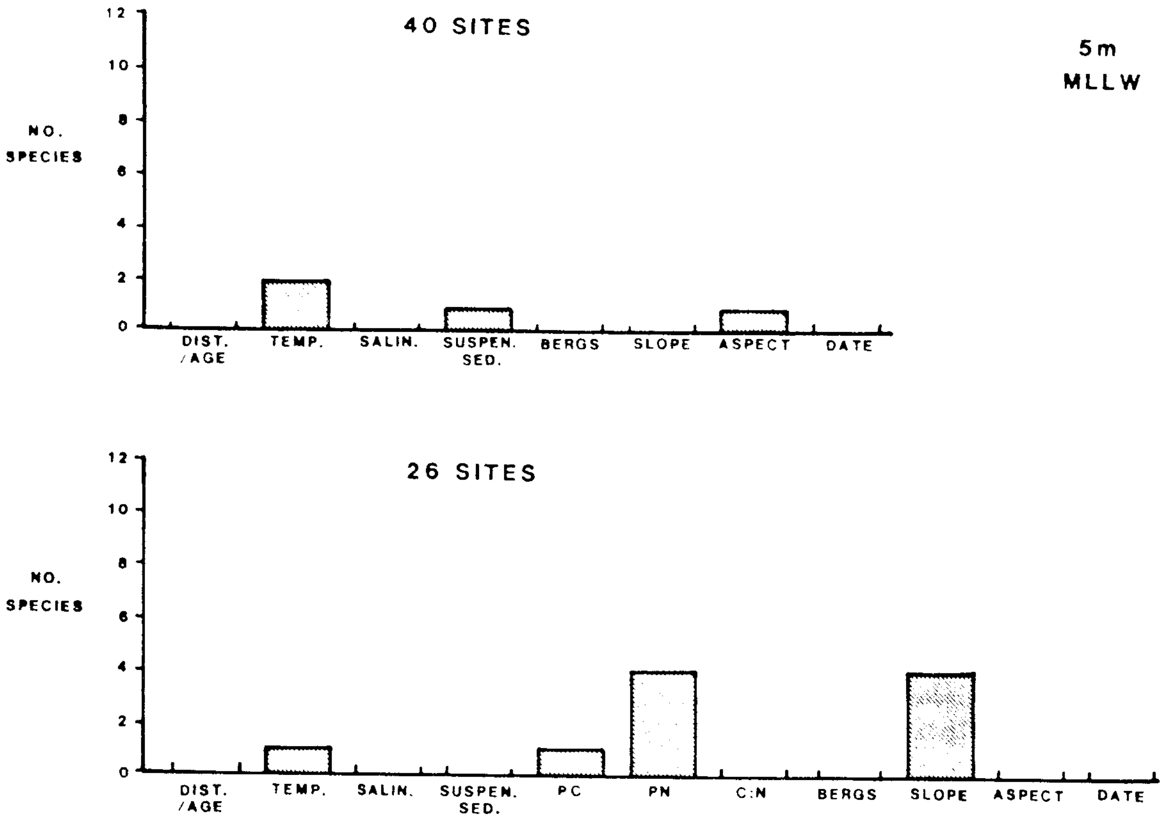


Figure 24e. Results from the 5 m MLLW vertical intertidal level.

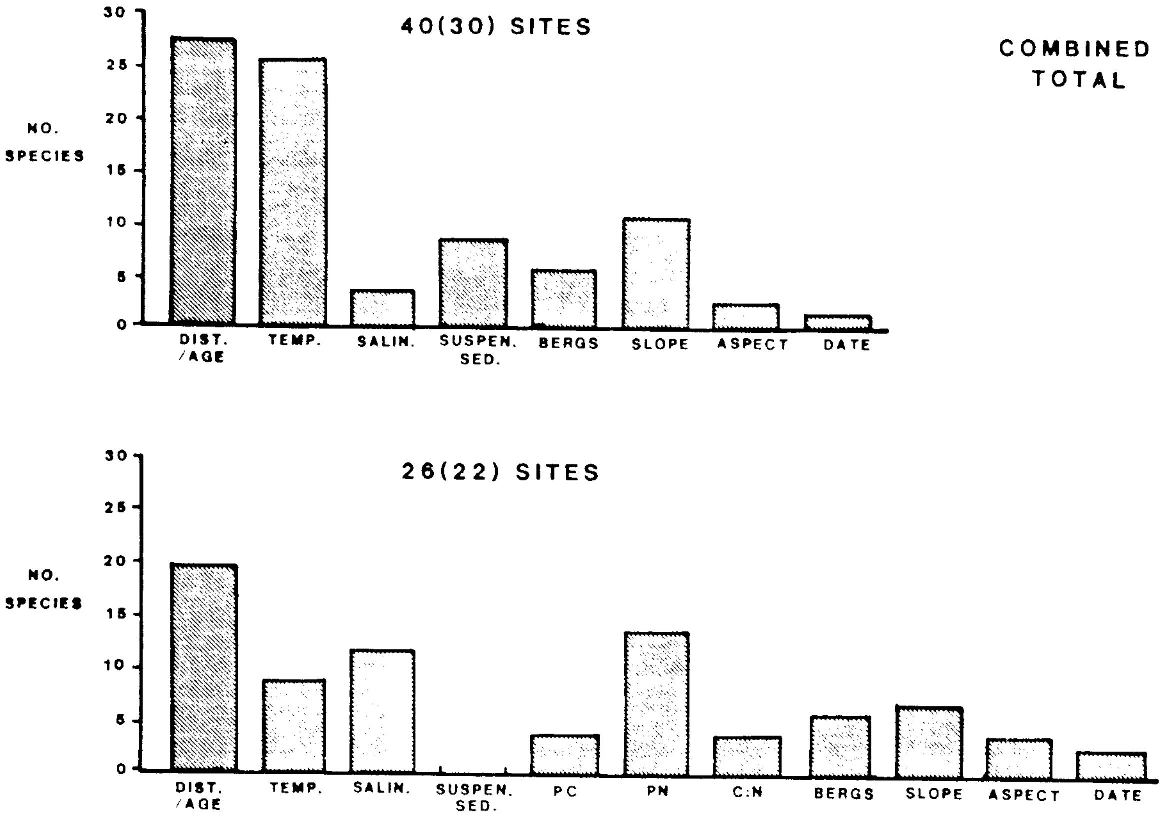


Figure 24f. Results from all vertical intertidal levels combined. Column heights are the sums of results from all individual levels (0 m through 5 m MLLW).

Table 5. Marine environmental factors most highly correlated with species richness (mean number of species per quadrat) and proportion of total unoccupied intertidal substrate surface among the 40 study sites. Results (from stepwise multiple regression analyses) for each vertical intertidal level are divided into those computed from the data set containing suspended particulate carbon and nitrogen measurements (n = 26 sites; 22 sites at 0 m) and those computed from the data set without those measurements (n = 40 sites; 30 sites at 0 m). "Suspend. Sed." refers to total suspended particulate concentration in seawater, and "PN" refers to suspended particulate nitrogen factors. "-" indicates that the proportion of total unoccupied surface showed no significant correlation with any environmental variable in the analysis (critical F = 4.000).

	0m		1.25m		2.5m		3.75m		5m	
	NO CN DATA (30 SITES)	INCL. CN DATA (22 SITES)	NO CN DATA (40 SITES)	INCL. CN DATA (26 SITES)	NO CN DATA (40 SITES)	INCL. CN DATA (26 SITES)	NO CN DATA (40 SITES)	INCL. CN DATA (26 SITES)	NO CN DATA (40 SITES)	INCL. CN DATA (26 SITES)
SPECIES RICHNESS	DIST. /AGE	PN	DIST. /AGE	DIST. /AGE	DIST. /AGE	WATER TEMP.	SUSPEND. SED.	SUSPEND. SED.	WATER TEMP.	DIST. /AGE
% TOTAL UNOCCUPIED SURFACE	WATER TEMP.	SALINITY	—	—	SUSPEND. SED.	DIST. /AGE	WATER TEMP.	WATER TEMP.	WATER TEMP.	PN

the factor that was most frequently identified as the best predictor of percent total unoccupied surface (Table 5).

The environmental parameters were much more important than sampling date in explaining patterns of species composition, species richness, and percent unoccupied space. For ten data sets (with and without particulate C and N data x five intertidal levels) for each species, sampling date was the best predictor of the distribution of a species only twice (Fig. 24f; Table 6; Appendix X).

The distributions of adult and juvenile (spat) *Balanus* spp. and *Thais lima* adults and eggs again were best predicted by the distance/age factor and water temperature (Table 7). When significant regressions were found, the same factor almost always was identified as the best predictor of both the adult and the juvenile/egg forms. In the lower intertidal zone (0-1.25 m) distributions of both species tended to be best predicted by distance/age, while higher in the intertidal (2.5-5 m) water temperature and, occasionally, suspended particulate N or C factors were the best predictors.

Species whose distributions most frequently correlated most strongly with the same environmental parameter can be grouped together (Table 6); species within such groups tended to respond similarly in their distributions to similar physical gradients. Overall, distance/age and water temperature most frequently were shown to be the best predictors of biological distributions. Distributions of Amphipoda spp. and the *Urospora/Ulothrix* spp. complex usually were best predicted by amount of total suspended particulates and particulate C:N ratio, while number of grounded ice fragments was exclusively the best

Table 6. List of intertidal species and the number of times a corresponding environmental parameter was shown by stepwise multiple regression analyses to be most highly correlated with the distributional pattern of each species. Only species for which at least one environmental factor was most highly correlated more than once are included. Numbers are based on results from ten data sets (with and without suspended particulate carbon and nitrogen data x five vertical intertidal levels) for each species, depending upon the number of intertidal levels at which a species occurred. A sum of less than ten for a species row indicates that the species did not occur at one or more intertidal levels, and/or significant correlation of the distributional pattern of the species with any environmental variable in the analysis (critical F = 4.000) did not occur in every data set. "Suspen. Sed." includes the factors of total suspended particulate concentration in seawater and extinction coefficient. "Bergs" means number of ice fragments.

SPECIES	DIST. /AGE	TEMP.	SALIN.	SUSPEN. SED.	PC	PN	C:N	BERGS	SLOPE	ASPECT	DATE
Collisella	5					2					
Hiatella	3										
Margarites	3	1							1		
Mytilus	3	1		1		1				1	
Thais adults	3	2	1			1					
Anthopleura	2										
Tealia	2										
Gigartina	2										
Brown filamentous	2										
Onchidella	2								1		
Notoacmaea	2		1						1		
Polysiph./Pterosiph.	2		1		2				1		
Thais eggs	2	1				1					
Balanus adults	2	2			1						
Littorina	2	2		2		1					1
Rhodomela	2	3	1								
Balanus spat	2	4				1			1		
Lithothamnium	1	3									1
Evasterias		3	1			1					
Serpula		2									
Acrosiphonia		2							2	2	
Halichondria										2	
Amphipoda				2			1				
Urospora/Ulothrix				3			3				
Enteromorpha			2	1				6			
Brown algal coating								6			

Table 7. Marine environmental factors most highly correlated with distributional patterns of *Balanus* spp. adults and juveniles (spat), and *Thais lima* adults and eggs at five vertical intertidal levels. Results (from stepwise multiple regression analyses) for each level are divided according to separate data sets used for computations, as in Table 5. "PC" and "PN" refer to suspended particulate carbon and nitrogen factors, respectively. "-" indicates that the distributional pattern of *Balanus* spp. or *T. lima* at that intertidal level showed no significant correlation with any environmental parameter in the analysis (critical F = 4.000). "X" indicates that *T. lima* was not encountered at that intertidal level.

	0m		1.25m		2.5m		3.75m		5m	
	NO CN DATA (30 SITES)	INCL. CN DATA (22 SITES)	NO CN DATA (40 SITES)	INCL. CN DATA (26 SITES)	NO CN DATA (40 SITES)	INCL. CN DATA (26 SITES)	NO CN DATA (40 SITES)	INCL. CN DATA (26 SITES)	NO CN DATA (40 SITES)	INCL. CN DATA (26 SITES)
BALANUS ADULTS	DIST. /AGE	DIST. /AGE	—	—	WATER TEMP.	—	—	—	WATER TEMP.	PC
BALANUS SPAT	SLOPE	DIST. /AGE	DIST. /AGE	WATER TEMP.	WATER TEMP.	—	WATER TEMP.	WATER TEMP.	—	PN
THAIS ADULTS	DIST. /AGE	—	DIST. /AGE	DIST. /AGE	WATER TEMP.	PN	WATER TEMP.	SALINITY	X	X
THAIS EGGS	—	—	DIST. /AGE	DIST. /AGE	WATER TEMP.	PN	X	X	X	X

predictor for *Enteromorpha* spp. and species making up the brown algal coating (Table 6).

The principal components analysis computed a score for each principal component (PC) for each intertidal level at each site. When these PC scores were regressed stepwise against all environmental parameters, a pattern emerged (Appendix XI) that was similar to results obtained from individual species regressions. Forty percent (20 of 50) of all PC scores showed no significant correlation with any measured environmental variable in the analysis. The 30 remaining PC scores were best predicted by water temperature (seven times), measures of suspended particulate C and N (six times), and the distance/age factor (five times).

DISCUSSION

Because of the close linear correlation between substrate age and distance from the glacier, correlation analyses cannot separate the relative importance of these two factors in determining biological community composition. Nevertheless, comparisons of the physical and biological trends along the distance/age gradient provides strong evidence that certain environmental factors probably are the major determinants of present-day intertidal community composition and degree of development in Glacier Bay.

Directional and predictable temporal patterns of species replacement occur in marine intertidal communities, just as they do in terrestrial ones (Haven 1971, Southward and Southward 1978, Sousa 1979a,b, Dean and Hurd 1980, Turner 1982, Gallagher *et al.* 1983, Greene *et al.* 1983, Lubchenco 1983, Niell and Varela 1984, Breitburg 1985, Keats *et al.* 1985). However, it is unlikely that substrate age alone controls degree of intertidal community development on the timescale of the entire transect (200 y) in Glacier Bay. Experimental and descriptive studies of marine succession on rocky intertidal substrates have shown that succession runs its entire course from totally bare surface to a fully developed "mature" community in a much shorter time, generally five to ten years at most (Haven 1971, Southward and Southward 1978, Sousa 1979a,b), suggesting that the physical environment is very important in controlling the pattern of development at Glacier Bay.

Physical Environment

Principal components analysis and correlation analysis of measured physical parameters yielded two coherent groups of factors: those that varied linearly with distance from the glacier and those that varied exponentially with distance. Linearly varying patterns are similar to those in most fjords. These include water temperature, salinity, air temperature, suspended particulate nitrogen (N) per volume seawater, suspended particulate carbon (C) and N on a percent weight of total particulates basis, and 1% light depth. Exponentially varying factors were related to extremely high inputs of suspended particulates and ice fragments at the head of the fjord, which are characteristics unique to tidewater glacial fjords. These include light extinction, total suspended particulates, percent silt coverage of intertidal surfaces, suspended particulate C per volume seawater, particulate C:N ratio, and number of grounded ice fragments. Relatively little detailed information is available regarding the physical components of tidewater systems. Because characteristics of the near-surface physical environment are central to determining patterns of intertidal community development, a thorough consideration of physical patterns is important.

Slope had the lowest correlation coefficient from principal components analysis, indicating that it was not an important determinant of patterns of other environmental parameters. Based on data plots, regression results, correlation matrix, and principal components analysis, it is unlikely that sampling date determined patterns of other environmental parameters. While sampling date was well correlated with other variables (which had relatively weak correlations with distance from the glacier) within its principal component and could have affected their patterns, it was not significantly correlated with distance. Thus, the data represent the true gradient from glacier to baymouth and are not an artifact of seasonal sampling.

I. Hydrography

A linear increase in near-surface summer water temperature and salinity with distance from the fjord head is common in fjords worldwide (Syvitsky *et al.* 1987). Similar gradients have been reported in Alaska for Port Valdez (Feder and Keiser 1980), Berners and Katlian Bays (Hood 1969), and several other fjords (Pickard 1967). The pattern in Glacier Bay has been described on a gross scale from widely-spaced occasional measurements by Pickard (1967), Quinlan (1970), Hoskin and Burrell (1972), Matthews and Quinlan (1975), Matthews (1981), Malme *et al.* (1982), Wing and Krieger (1982), and Krieger and Wing (1984). In general, published surface water temperature and salinity measurements agree with mine, indicating that the horizontal patterns I observed in 1983 and 1984 adequately represent the usual pattern at Glacier Bay. This relationship apparently is caused by mixing of the cold, fresh water entering at the heads of the inlets with more oceanic water of higher temperatures and salinities at the fjord mouth.

Temperature decreases and salinity increases with depth reported by other workers also are similar to patterns I observed. Again, this trend probably results from the effect of mixing with underlying denser water of lower temperature and higher salinity. In Glacier Bay, the exception of water temperature increasing with depth near the glacier is due to extremely low surface salinities which allow colder water (meltwater originating from the tidewater glacier face) to maintain lowest density at the surface.

Among-site variation of temperature and salinity tended to be less at lower depths than at the surface because surface conditions are influenced more strongly by spatially and temporally variable ambient air temperatures, insolation, and precipitation. Narrower vertical temperature and salinity ranges with increasing distance from the head of the fjord were reported by Feder and Keiser (1980) for Port Valdez. Those patterns, as well as data provided by P.R. Miles (personal communication) for Glacier Bay in 1981 and 1982, show trends similar to my 1984 observations. This pattern probably is best explained as the result of increasing time and exposure to wind and marine mixing forces with distance from the head of the fjord, as well as the previously described vertical mixing effect.

II. Suspended particulates

Muir Inlet annually receives more sediment, approximately nine m/y, than any other known glacial fjord and perhaps any sedimentary environment (Mackiewicz *et al.* 1984). This explains the high values for total particulates that I measured close to the glacier (up to 159 mg/L; Appendix IV). Thus, if sediment load is an important factor determining community composition in glacial fjords, it should be clearly evident in

Glacier Bay. Similar high values of total suspended particulates have been reported from the head of Queen Inlet in the western arm of Glacier Bay (1025-5810 mg/L; Hoskin and Burrell 1972) and from the head of Port Valdez (up to 421 mg/L; Keiser 1978, Feder and Keiser 1980).

Most of the suspended particulate material consists of sand and silt. Upon entering the fjord, the larger, heavier particles settle out of suspension in the water column most rapidly, while the finer size fractions remain in suspension and are carried farther out the bay. Flocculation of particulates as they enter the marine environment further speeds settling (Hoskin and Burrell 1972). The total flux of material to the bottom rapidly decreased from a maximum of 2.4 m/y at the extreme upper end of Queen Inlet of Glacier Bay to 0.4 m/y at the Inlet's mouth, a distance of less than six km (Hoskin *et al.* 1976). This explains the exponential decrease in total particulates I observed across 15 km near the face of Muir Glacier.

Howe Sound (a non-tidewater glacial fjord) in British Columbia provides a contrasting situation, with summer concentrations of 1.8 to 4.7 mg/L for near-surface waters (Syvitsky 1980). In addition to being comparatively low, these values decreased linearly with distance from the head of the fjord, in contrast to the exponential decrease observed at Glacier Bay. I suspect that the majority of runoff entering the head of Howe Sound flows from relatively stable streams which do not carry the extremely high suspended sediment concentrations typical of fjords with tidewater glaciers or near-tidewater glaciers terminating in mudflats with turbid outwash streams. Thus, at Glacier Bay the exponential relationship between particulate-related factors and distance from Muir Glacier probably reflects the glacier's tidewater nature.

Glacial fjords have higher concentrations of suspended particulate organic carbon (POC; 0.1 - several mg/L) than do non-glacial Alaskan marine waters (Loder 1971). Those values, however, usually are a small fraction of very high total particulate concentrations. Very low percentages of carbon (C) in total particulates in young, recently deglaciated fjord systems probably are due to lack of vegetation in areas of meltwater runoff (Loder 1971). Although I analyzed samples from Glacier Bay for total (organic + inorganic) particulate C, the inorganic contribution probably was insignificant. Ugolini (1967) measured a maximum of 5% $CaCO_3$ by weight in mineral soils collected at Glacier Bay; by calculation this proportion yields a total of only 0.6% C. Also, Hong (1986) measured mean values of approximately 1% inorganic C in suspended particulates from Boca de Quadra, a non-tidewater glacial fjord in southeastern Alaska.

In Glacier Bay, the exponential decrease of particulate C with distance from the glacier is best explained by its close correlation with total particulates ($r = 0.76$; Table 1). Those two factors also occurred together within one of the principal components (PC1) generated by the principal components analysis of environmental parameters (Table 2). With such high concentrations of total particulates in the near-glacier water, even very low concentrations of inorganic C (from $CaCO_3$ in sediment parent material) or possibly fossil organic C (interstadial plant material washed out of sediments in which it has been buried and preserved) from beneath the glacier could produce high values on a per-volume seawater basis. By contrast, when all Alaskan marine waters were considered (Loder 1971), POC correlated more closely with salinity and particulate N concentration, because those parameters are associated with plankton production, which is the usual source of POC in marine ecosystems.

The linear increase in near-surface particulate nitrogen (N) concentration in seawater with distance from the glacier probably is due to increasing marine productivity which is in turn related to less stressful conditions of temperature, salinity, total particulates, and light extinction closer to the baymouth. The particulate N content of glacial meltwater of other Alaskan fjords is (as with POC) much less than that of marine source waters (Loder 1971).

The linearly increasing trends of percent concentration of particulate C and N in total particulates in Glacier Bay similarly are best explained by the gradient of transition from the largely mineral terrestrial source of particulates to the largely biogenic marine source with increasing distance from the glacier. As total particulate concentration decreases, its composition becomes less dominated by mineral material, and organic particulates (*i.e.*, phytoplankton, detritus, *etc.*) contributed by more oceanic conditions and better vegetated terrestrial communities comprise a greater proportion of the total amount.

The exponential relationship between suspended particulate C:N ratio and distance from the glacier probably is again due to extremely high amounts of total particulates near the glacier that contain low concentrations of inorganic or fossil organic C. Carbon:nitrogen ratio and total particulates were closely correlated ($r = 0.82$; Table 1). Those two factors also occurred together (along with particulate C and other parameters that decreased exponentially with distance) within one of the principal components (PC1) generated by the principal components analysis of environmental parameters (Table 2). The high C:N values of 30 to 40 (Fig. 7e; Appendix IV) are higher than would be expected, even though terrestrially derived particulate organic material usually has a C:N ratio of at least 12 (Meyers *et al.* 1984). Relatively large amounts of inorganic or fossil organic C (compared to amounts of N) as a constituent of total suspended particulates very near the glacier could explain the high C:N ratios. When particles rapidly settled out of suspension as they were carried out the fjord, most of this near-glacier C and N would be removed and replaced by marine-derived biogenic material. The remaining C:N values of 5 to 7 measured beyond ten km from the glacier are comparable to typical values from biogenic marine detritus and phytoplankton; the mean C:N ratio of biogenic particulates in the open ocean is 6 (Redfield *et al.* 1963).

It appears that the factors of mixing and greater biological productivity act simultaneously to produce the distance-related patterns of suspended particulates in Glacier Bay. The region close to the glacier has a very high input of total particulates which contain low C concentrations and virtually no N. The majority of those particles rapidly settle out of suspension with distance from the glacier and are replaced by biogenic marine particles as the marine environment becomes increasingly productive in response to higher temperatures and salinities, greater transparency and photic depth, and closer proximity to rich coastal zone waters. Coupled with a greater contribution of organic detritus *via* runoff as terrestrial communities become better developed along the same gradient, total particulate composition becomes richer in proportions of C and N and normal in marine C:N ratio.

Percent silt covering intertidal surfaces also decreased exponentially with distance from the glacier. This pattern is due to the length-of-bay pattern in total particulates which is the source of settled silt on rock surfaces. The asymptotic "thresholds" of those two parameters (15 km from the glacier for total particulates; 35-45 km from the glacier for silt covering) probably were different because a large proportion of suspended sediment measured close to the glacier consisted of larger grain sizes that settled out of the water column most rapidly. Silt-size particles were carried farther out the bay, coating a portion of intertidal surfaces to a thickness of at least 0.5 cm out to approximately 40 km from the glacier.

III. Light

Light extinction, measured by both Secchi disc and light meter, is another parameter that decreased exponentially with distance in Glacier Bay and was controlled primarily by suspended mineral particulates in the inner portions of the bay. Hale and Wright (1979) believe that suspended sediment (as opposed to plankton production) is the most important determinant of turbidity in inner Glacier Bay. Pickard (1967) reported Secchi depths that increased with distance from the heads of several southeastern Alaskan fjords. Carpenter (1983) reported similar distance-related patterns of Secchi depth and 1% light depth in Aialik Bay, a tidewater glacial fjord. She attributed those patterns to a corresponding decrease in amount of suspended particulates with distance from the glacier.

IV. Ice fragments

Pickard (1967) also noticed a distance-related gradient for numbers of ice fragments within Alaskan tidewater glacial fjords. The exponential relationship I observed in Glacier Bay was due in part to the linear increases in water and air temperatures with increasing distance from the glacier. More importantly, however, as ice fragments melt and become smaller, the ratio of surface area to volume decreases, so that they melt ever faster with respect to their size. Consequently, they tend to rapidly disappear as an exponential function of distance/time since calving.

In summary, data I collected were consistent with the relatively few published studies of the physical environment of tidewater glacial fjords. These data indicate that the patterns observed in the year of study at Glacier Bay were similar to previously observed patterns at Glacier Bay and are representative of patterns in other tidewater glacial fjords. Tidewater glacial fjords are unique in having a high suspended sediment load that decreases exponentially with distance from glaciers; they are similar to most northern fjords in general in that water temperature and salinity change linearly from the head to the mouth of the fjord. The clear dichotomy between patterns of environmental factors related to presence of a tidewater glacier *vs.* patterns common to most fjords sets the stage for consideration of which environmental factors most strongly determine marine community development in Glacier Bay.

Biological Commmunity

I. Species richness patterns

Intertidal species richness increased linearly with distance from Muir Glacier at all intertidal levels, suggesting that either substrate age or linearly varying parameters of the marine physical environment are the primary determinants of biological diversity. As previously discussed, the rapid rate of community development (5-10 y) that has been documented in the intertidal zone in other studies makes it unlikely that substrate age could explain the linear increase in species richness over the 200 y transect at Glacier Bay. The increasing trend of species richness with distance was expected based on Mueller's (1973) species list. Relative numbers were much higher in Mueller's work, however, because his data represent lists of all species encountered at a site, as opposed to quantitative samples. In addition, Mueller identified organisms to the species level more frequently than I did, and his sites included a variety of intertidal habitats (solid bedrock outcrops, boulder beaches, sandy areas, and mudflats), while I studied only bedrock outcrops. Increasing diversity of pelagic zooplankters and subtidal benthic organisms with distance from a tidewater glacier has also been reported for Aialik Bay (Carpenter 1983). This pattern was attributed to less severe marine environmental conditions with increasing distance from the glacier.

The more rapid distance-related species richness increases observed at lower intertidal levels (0 and 1.25 m) as compared to higher levels can be due to the relative proportions of time spent submerged during each tidal cycle. Organisms at lower levels are submerged for longer periods and should be more strongly affected by marine physical factors than those organisms living higher in the intertidal zone. This different pattern of response between communities which were initially exposed by the receding glacier at the same rate is additional evidence that physical gradients of the marine environment are more important determinants of community development than is substrate age.

An alternative explanation for vertical patterns of species richness is based on the idea that lower intertidal communities, with their relatively constant marine influence (*e.g.*, water temperature, salinity, oxygen, and food) and lower levels of physiological stress (*e.g.*, desiccation and extreme air temperatures) and physical disturbance (*e.g.*, wavewash and scouring), generally are more stable because of greater environmental constancy and predictability. Long-term biological succession could be expected to proceed at a more rapid rate (with an associated increase in species richness) in such "biologically accomodated" lower intertidal communities than in more "physically controlled" upper level communities (Sanders 1969, Slobodkin and Sanders 1969). Results from the dowel experiment do not support this hypothesis, however, because dowels were dislodged to equal degrees at all intertidal levels at a given site.

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II. Effects of physical disturbance

The amount of substrate colonized appears to be determined by the physical disturbance regime as evidenced by the similar curvilinear distance-related patterns of area of unoccupied surface and rate of dowel loss. Greatest amounts of unoccupied space and mechanical disturbance were recorded for sites close to the glacier and sites near the baymouth at the opposite end of the gradient.

A high level of disturbance occurred near the glacier where frequent calvings of ice from the tidewater glacial face produce large swells that create considerable wavewash across shores up to two km away. More importantly, numerous floating ice fragments that are introduced into the fjord in this way continually bump along the shoreline as they are carried up and down the inlet by tides, winds, and currents. Ice fragments weighing tens to thousands of kg frequently become grounded in the intertidal zone as the tide recedes, crushing intertidal organisms beneath them. This "scour zone" extends out to approximately 15 km from the glacier. Ice scour has been described as a major physical disturbance to marine benthic biota at other high latitude locations (Wilce 1959, Ellis and Wilce 1961, Stephenson and Stephenson 1972, Keser 1978, O'Clair *et al.* 1979, Hooper 1981, Cimberg 1982, Mathieson *et al.* 1982, Bolton 1983, Keser and Larson 1984, Keats *et al.* 1985).

Ice scouring is virtually nonexistent close to the mouth of Glacier Bay, but mechanical disturbance in the form of wavewash becomes important because of increased exposure to the relatively open waters of

Icy Strait. Occasional and limited scouring by floating debris (logs and other coastal flotsom) can contribute to disturbance at baymouth sites. This high level of physical disturbance affects the intertidal community in ways similar to those of the near-glacier situation, maintaining a significant portion of the substrate surface clear of biological establishment. The two agents of disturbance (scouring and wavewash) differ at opposite ends of the fjord, but their effects on the intertidal community are similar. The central portions of the distance/age gradient are relatively protected from both disturbance regimes, and communities there are able to more fully utilize the available substrate.

III. Community organization

Because there was little agreement between the biological principal components analysis results calculated from the two sets of frequency data and coverage/abundance data, factors permitting a species to occur at a site probably are not highly correlated with factors determining its coverage or abundance. The additional result of species "groupings" varying widely among vertical intertidal levels suggests that the factors causing differences in community composition along the vertical gradient of intertidal height differ from factors determining community composition along the horizontal distance/age transect from glacier to baymouth. Furthermore, because approximately half of the species distribution patterns were not significantly correlated with any environmental variable in stepwise multiple regression analyses, those patterns were not related to the strong physical gradient from glacier to baymouth in any simple fashion. Stepwise regression results also indicated that sampling date was of little importance in explaining patterns of species composition, species richness, and percent unoccupied surface, and thus did not contribute significantly to biological patterns along the distance/age transect.

For *Balanus* spp. and *Thais lima*, distribution patterns of juveniles and eggs were analyzed along with those of adults. Results indicate that for both species the patterns of both adults and juveniles/eggs are affected most strongly by the same environmental factor (either distance/age or water temperature, depending upon which data set was used). *Balanus* spp. juveniles peaked in coverage farther from the glacier than did adults, suggesting that juveniles are more sensitive to environmental stresses associated with close proximity to the glacier.

Glacier Bay intertidal communities are exposed to a number of different stresses resulting in a variety of individual species distributions along environmental gradients. Analyses of such biological and physical gradients with respect to one another, together with consideration of biological interactions, provide insights into the relative importance of environmental factors to aspects of intertidal community development. Certain species and species groups in Glacier Bay provide particularly helpful illustrations of the ways in which physical and biological factors can interact to determine community organization.

A) *Evasterias troschelii*, *Thais lima*, *Littorina sitkana*, and *Collisella* spp.: predators and grazers sensitive to low salinity

Compared to most other marine phyla, echinoderms are stenohaline, tolerating little change in the salinity of their environment (Binyon 1961, 1966). Moreover, their salinity requirement is relatively high (25-35‰), approximating normal oceanic seawater (Binyon 1961). The narrow tolerance range is due to the fact that echinoderms have little or no osmoregulatory ability; they lack any morphologically differentiated excretory structures and thus are isosmotic, losing salts and gaining water by diffusion across the integument and stomach wall at low salinities (Binyon 1961, 1966, Gardiner 1972). Asteroid larvae, as well as adults, also are sensitive to reduced salinities (Thorson 1946).

The most euryhaline asteroids, *Asterias* spp., have minimum salinity tolerances of 15 to 25‰ for reproductive populations. Most of these occur in the Baltic and Black Seas, where the seawater has been gradually diluted over geological epochs, allowing biological acclimatization (Binyon 1966, Feder and Christensen 1966). Experimental studies also have shown lower limits of salinity tolerance to fall within this range (Binyon 1961, 1966).

Intertidal echinoderms in Alaskan waters have similar minimum salinity tolerances. *Evasterias troschelii*, one of the most important predators in intertidal communities in Glacier Bay, did not occur closer than 45 km from the glacier (Fig. 17). This distributional limit was marked by a near-surface (mean for measurements from 0-7.5 m) salinity maximum of approximately 24‰; the actual surface salinity there was approximately 21‰ (Appendix III). Cimberg (1982) reported a surface salinity biological threshold of 15‰ in Boca de Quadra; *Balanus glandula* and *Mytilus edulis* could exist at salinities lower than this threshold, but the predatory sea star *Pisaster ochraceus* (which feeds on barnacles and mussels there) could not. A similar situation was reported for Berners Bay, where *M. edulis* extended its vertical intertidal range to 5 m below MLLW where *E. troschelii* was excluded by low-salinity (9.8‰) surface water (Calvin 1977). Also excluded from the low-salinity Berners Bay site was *Strongylocentrotus droebachiensis*, another echinoderm. *E. troschelii* and *S. droebachiensis* were present only at an outer site (surface salinity > 10‰ in summer) at the lowest intertidal level studied in Port Valdez (Feder and Keiser 1980, Rucker 1983); their absence from sites very close to the head of the fjord was attributed to conditions of low salinity, although barnacles and mussels were able to persist there.

Some soft-bodied gastropod molluscs (*Aplysia* spp., some nudibranchs) are osmoconformers, adapting to a broad range of salinities (Prosser 1950, Gardiner 1972). The predatory snail *Thais lima*, however, is not known to possess this ability and had a distributional limit in Glacier Bay (45 km from the glacier; Fig. 18) similar to that of *E. troschelii*. The limit corresponds to a minimum surface salinity of approximately 21‰ (Appendix III). *T. lima* also was excluded from the previously described Berners Bay site of low surface salinity (9.8‰; Calvin 1977). In Glacier Bay, the gastropod molluscs *Littorina sitkana* and *Collisella* spp. are important algal grazers whose distributions extend (with markedly reduced abundances) to near-glacier sites with low near-surface salinities (approximately 18‰; Fig. 5b; Appendix III). Despite the fact that algal coatings and *Fucus distichus* maintained near-glacier densities that were adequate to support larger populations of grazers, other environmental factors apparently held down grazer numbers. Low salinity could be one of those factors, along with low water temperature and high levels of suspended sediment and ice scour. In the Baltic Sea, *Littorina obtusata* adults had a minimum salinity tolerance of 12 to 13‰, and *L. littorea* eggs had a minimum tolerance of 15‰ (Remane and Schlieper 1971).

B) *Balanus* spp. and *Mytilus edulis*: near-glacier response to the interaction of physical stresses, competition, and predator exclusion

1. Decreased absolute abundances: direct effects of the physical environment

The low absolute abundances of both *Balanus* spp. and *M. edulis* at sites extremely close to the glacier can be explained in terms of direct responses to the physical stresses of high suspended particulate levels and low water temperature and salinity. Rucker (1983) reported extensive adult mortality (37.9%) of *Balanus balanoides* at a site adjacent to a turbid outwash stream at the head of Port Valdez, which she attributed to heavy silt load deposition on intertidal surfaces following a period of high precipitation with high runoff. Barnacles were covered by silt and apparently were unable to feed effectively. Feder and Keiser (1980) attributed greater set of barnacle spat at sites farther from the head of Port Valdez than at the site closest to the head to high sediment deposition in summer.

Mytilus edulis is also susceptible to high levels of suspended sediment in the water column. Loosanoff *et al.* (1966) and Davis and Hidu (1969) found that turbidity caused by high suspended particulate levels can limit the depth of primary production and thus food for larvae. *M. edulis* is a nonselective filter-feeder, and must spend more energy processing particulate material to obtain adequate food when suspended particulate levels are high (Foster-Smith 1975). This can translate into slower growth rates in more turbid waters. At near-glacier locations in Glacier Bay, low total particulate nitrogen concentrations and low nitrogen weight percentages of total particulates probably exacerbate the "food dilution" problem for *M. edulis* and other filter feeders. Nitrogen is one of the most (if not the single most) important limiting nutrients essential to biological productivity in coastal marine ecosystems (Ryther and Dunstan 1971, Raymont 1980, Nixon and Pilson 1983). *M. edulis* grew faster at the site of lowest suspended particulate levels in Port Valdez (Keiser 1978), and grew more slowly in the highly sedimented (11-278 mg/L) Wadden Sea than in less turbid Danish waters (Theisen 1973). In addition, sediments accumulating on intertidal substrates can interfere with mussel settlement patterns (Keiser 1978).

In general, it appears that high suspended particulate levels can adversely affect many intertidal filter-feeding species. In addition to the specific references to mussels and barnacles previously cited, Levinton (1982) reported that high suspended sediment inhibits feeding efficiency and deters growth of suspension feeders as a group.

Low water temperature adversely affects the survival and development of larval stages of *Balanus* spp. (Scheltema and Williams 1982) as well as feeding rate in adults (Southward 1964a). Water temperature is one of the environmental factors that correlated most strongly with distributions of adult and juvenile barnacles in Glacier Bay, particularly at higher intertidal levels.

Mytilus edulis persisted only at very low abundance at sites extremely close to the glacier. Low water temperature adversely affects the survival and development of larval stages of *M. edulis* (Hrs-Benko and Calabrese 1969, Seed 1969). Effects of delaying spawning (Seed 1969), reducing metabolic rate and feeding activities (Keiser 1978), and slowing growth (Boetius 1962, Seed 1969, Keiser 1978) in adults also have been attributed to low temperatures.

Geraci and Romairone (1982) reported adverse effects of low salinity on larval barnacle settlement. Hrs-Benko and Calabrese (1969) reported adverse low salinity effects on *M. edulis* larvae. *M. edulis* apparently is an osmoregulator and has a wide salinity tolerance (Prosser 1950), as low as 4 to 5‰ in the Gulf of Finland (Gardiner 1972). However, low salinity is stressful to *M. edulis*, particularly as it reduces metabolic rate and feeding activities, leading to slower growth (Bøhle 1972, Gardiner 1972, Keiser 1978), effects similar to those of temperature. From the standpoint of predation, however, low salinities can benefit mussels and barnacles by excluding predatory sea stars and snails, as will be discussed shortly.

Low salinities also can be a problem for other intertidal species. In general, species penetrate estuaries to their limits of tolerance to low and rapidly changing salinity conditions, and freshwater runoff can cause physiological stress in intertidal communities (Sumich 1980). Low near-surface salinities can change the vertical levels of establishment of intertidal algae (Druehl 1967), as well as disrupt normal phototactic responses in invertebrate larvae, causing reduced settling success (Carefoot 1977). Where the surface freshwater lens is as thick as the intertidal zone, less tolerant species are absent or restricted to the subtidal (Carefoot 1977).

2. Vertical zone depression: indirect effects of the physical environment

Depression of the *Balanus* spp. and *Mytilus edulis* zones to lower intertidal levels at sites close to the glacier can be a response by the barnacles and mussels to the more stressful physical environment and to activities of their predators. The upper limit of vertical intertidal distributions of organisms is controlled primarily by physical stresses associated with exposure to the air, while lower limits usually are controlled by biological interactions such as competition or predation (Connell 1961, Paine 1974). Establishment lower in the intertidal can minimize the cumulative effect of the usual stresses of frequent exposure to the air which are compounded by submergent physical stresses associated with close proximity to the glacier (*e.g.*, low water temperature and salinity, high suspended sediment). Establishment in the lower intertidal normally would put *Balanus* spp. and *M. edulis* at risk of greater predation by their major predators (in Glacier Bay) *Evasterias troschelii* and *Thais lima*. As previously mentioned, however, these two predators did not occur closer than 45 km from the glacier. Lower limits of *M. edulis* along the Washington coast typically are determined by competition with *M. californianus* and by predation, but Suchanek (1978) found that at Torch Bay, Alaska (on the outer coast near Glacier Bay) where *M. californianus* does not occur, the lower limit of *M. edulis* is instead exclusively determined by *E. troschelii* and four species of *Thais*, including *T. lima* which is the species that occurs in Glacier Bay. This predator-controlled lower limit is analogous to Paine's (1974) example of *M. californianus* and the predatory sea star *Pisaster ochraceus* on the Washington coast.

Space is the primary limiting resource for which intertidal organisms compete (Connell 1961, Dayton 1971, Paine 1974, Sutherland 1974, Menge 1976, Lubchenco and Menge 1978, Hastings 1980). Intertidal organisms respond to high levels of ice scour on rocky substrates by taking refuge in rock crevices or in spaces between and beneath boulders (O'Clair *et al.* 1979). Thus, even though a high proportion of total rock surface remains unoccupied close to the glacier, competition almost certainly occurs for relatively rare safe establishment sites, and the extension of *Balanus* spp. and *M. edulis* zones to lower intertidal levels can reflect such competition in the absence of predators.

Elsewhere, a similar response by *M. edulis* to the absence of predators has been reported for nearby Berners Bay (Calvin 1977). A third example of intertidal zone depression is from the Baltic Sea, where displacement of primarily bivalve communities to greater depths, termed "brackish-water submergence" (Remane 1955), has been observed. Both upper limit and lower limit vertical depressions occurred. Upper limit depression was attributed to a retreat from low surface salinities to less stressful salinities at greater depth; lower limit depression was described as a response to the combination of lack of competition in generally depauperate Baltic benthic communities and absence of predatory sea stars and snails (Remane and Schlieper 1971).

In Glacier Bay, the persistence of barnacles, mussels, and other organisms at sites with high levels of physiological and mechanical disturbance near the glacier indicates that they are highly stress-tolerant and are effective colonizers. High disturbance frequency leads to low diversity primarily because it prevents late-arriving and slowly growing species from occupying safe sites where they can become established (Connell 1978). *M. edulis* is tolerant of a wide range of environmental conditions (Seed 1969), which probably explains its broad horizontal and vertical ranges in Glacier Bay.

C) *Fucus distichus*: near-glacier response to the interaction of reduced grazing pressure, competition, and ice scour

The fact that *F. distichus* at lower intertidal levels was most successful close to the glacier probably is best explained in terms of biological interactions involving grazing and competition. Particularly at the 0 m level, distributions of coverage of *F. distichus* and abundance of *Littorina sitkana* varied inversely with respect to one another. *L. littorea* is the most important intertidal herbivore on the north Atlantic coast of North America (Lubchenco 1978, Lubchenco and Menge 1978), and its feeding activities exert considerable influence upon upper intertidal communities (NUSC 1981). It appears that the decline in grazing pressure with reduced abundance of *L. sitkana* at sites close to Muir Glacier in Glacier Bay allows a positive response of increased *F. distichus* growth at lower intertidal levels. Abundance of the grazing limpet *Collisella* spp. also markedly declined close to the glacier. Reduced abundance of both grazers probably results from environmental stresses associated with close proximity to the glacier, as previously discussed. Experiments involving removal of limpets from the intertidal in the Atlantic have shown that fucoid density significantly increases as a result (Jones 1948, Lodge 1948, Southward 1953, 1956, 1964b). Apparently, grazers exert this effect primarily by consuming newly settled sporelings; grazing is not a major source of mortality for mature plants (Keser 1978, Lubchenco 1978, Keser and Larson 1984), although it can slow their growth (Keser and Larson 1984). Adult plants usually are removed by extrinsic physical factors such as winter storms and ice scour. In upper Glacier Bay, ice fragments provide this source of disturbance.

The lower level pattern of increased *F. distichus* coverage also can be a result of decreased competition for light or space by other algae close to the glacier. Removal of *Chondrus crispus* and *Ascophyllum nodosum* from the lower intertidal zone permitted dense settlement of *Fucus* spp. on the northern Atlantic coast; those species normally excluded *Fucus* spp. by competition (Lubchenco 1980, Keser and Larson 1984). All other algal species in Glacier Bay except *Enteromorpha* spp., the *Urospora/Ulothrix* spp. complex, and various benthic diatom assemblages which form coatings markedly decreased in coverage close to the glacier. Those algae probably are unable to survive the stresses of ice scour (Ellis and Wilce 1961, Keser 1978, O'Clair *et al.* 1979, O'Clair 1981, Cimberg 1982, Mathieson *et al.* 1982, Keser and Larson 1984, Keats *et al.* 1985), low salinity (Druehl 1967, Cimberg 1982), and reduced light available due to increasing turbidity.

SUMMARY

Substrate age and distance from Muir Glacier are closely and linearly correlated ($r^2 = 0.99$), making it difficult to separate the two effects based solely on statistical correlation analyses. Gradients of near-surface marine physical factors were strong, varying from cold, fresh, sediment-laden water very near the glacier to warmer, more saline, and less turbid oceanic conditions toward the mouth of the bay. The intertidal biological community likewise exhibited clear distance- and/or age-related trends in both species richness and community composition.

Results of environmental measurements can be grouped into those that varied in a linear fashion with distance, and those that varied exponentially. Linear factors include water temperature, salinity, air temperature, suspended particulate nitrogen (N) concentration in seawater, suspended particulate carbon (C) and N on a percent weight total particulates basis, and 1% light depth, all of which increased from glacier to baymouth. Water temperature and salinity decreased and increased, respectively, with depth. Both decreased in variability with depth and with distance from the glacier. Factors that decreased exponentially along the same transect include total suspended particulates and particulate C concentration in seawater, particulate C:N ratio, light extinction coefficient, number of grounded ice fragments, and percent intertidal substrate surface covered by $\geqq 0.5$ cm

glacial silt. Suspended particulate parameters generally showed no clear and consistent vertical trends.

The linear patterns of water temperature and salinity along the horizontal distance gradient are a result of mixing with warmer, more saline oceanic water at the mouth of the bay. Vertical trends similarly can be ascribed to underlying oceanic water. Decreasing variability among sites with increasing distance from the glacier probably is due to the greater degree of exposure to wind and marine mixing forces toward the more open mouth of the bay.

Total suspended particulate concentration in seawater decreased exponentially with distance from the glacier because particles rapidly fall out of suspension when sediment-laden meltwater enters the head of the fjord and quickly loses its energy. Particle flocculation also plays a role. Light extinction and percent silt coating were directly related to total particulates. Particulate C concentration in seawater and C:N ratio also were correlated with total particulates; additionally, there was the possibility of inorganic and/or fossil organic C as components of total particulates. Ice fragments melt as a function of surface:volume ratio, so that the relative melting rate increases exponentially with decreasing size.

Results from the dowel experiment suggest that physical disturbance controls the area of unoccupied intertidal substrate surface. Proportion of bare substrate generally was high at the extreme ends of the glacier to baymouth transect, and lowest in the middle portion of the bay. Dowels were dislodged in a similar pattern, indicating highest disturbance levels close to the glacier (ice scouring) and near the baymouth (wavewash due to exposure). Lowest level of disturbance and least amount of bare surface in the mid-bay region suggest that this portion of the transect is best protected from mechanical disturbance agents of scour and heavy wavewash.

Intertidal community composition changed dramatically with distance/age. Anemones, chitons, echinoderms, predatory snails, and hermit crabs are prominent species that were limited in distribution to the outer half of the bay. Other species (barnacles, mussels, limpets, littorine snails, rockweed) extended all the way to sites very near the glacier, but almost all decreased in coverage or abundance. Species richness increased linearly with distance/age. Stepwise multiple regression analyses showed that the distance/age factor usually was the best environmental predictor of individual species distributional patterns, followed by water temperature, salinity, and suspended particulate N factors. The same factors generally were shown to be most important in describing patterns of species richness, percent unoccupied substrate surface, and principal component scores.

Although the distance/age factor was the best predictor of intertidal biological community development patterns, it seems unlikely that substrate age is the critical component. It has been shown by other workers that marine intertidal succession proceeds much more rapidly than could explain the entire length-of-fjord pattern in Glacier Bay (5-10 y *vs.* 200 y). Distance from the glacier and the other linearly correlated marine environmental factors of water temperature, salinity, and suspended particulate N factors probably are the most important determinants.

Balanus spp. and *Mytilus edulis* zones were depressed to lower vertical intertidal levels at sites close to the glacier. This can be explained as a biological response to two general conditions: (a) physiological stress from desiccation at the upper distributional limits was minimized to better cope with other stresses associated with the near-glacier physical environment, and (b) major predators (*Evasterias troschelii* and *Thais lima*) did not extend beyond the middle portion of the bay, allowing *Balanus* spp. and *M. edulis* to expand downward in their vertical distributions to compete for limited establishment sites that were protected from ice scour.

Fucus distichus at lower vertical intertidal levels was more successful close to the glacier than farther away. The two-fold explanation for this pattern is: (a) it was a positive response to lower abundance of *Littorina sitkana* and *Collisella* spp. and thus reduced grazing pressure, and (b) there was decreased competition for space from other species unable to survive near-glacier conditions of low temperature and salinity, high turbidity, and/or heavy ice scour.

Almost all species whose distributions extended the full length of the bay existed in decreased coverage or abundance close to the glacier. This also is best explained by inability to effectively cope with environmental stresses of low temperature and salinity, and high suspended sediment load, turbidity, and ice scour.

In summary, it is clear that physical factors of the near-surface marine environment exert profound effects upon degree of intertidal community development in Glacier Bay. Effects related to biological succession probably are restricted to the first decade or so following initial exposure by receding glaciers. In particular, the presence of tidewater glaciers is extremely important because of the strong physical gradients established by their input of cold, fresh, heavily sediment-laden water and ice fragments at the heads of inlets. Various levels of physical and physiological stress exerted by combinations of these factors, together with related biological interactions, determine the abilities of species to establish and grow successfully along the glacier to baymouth continuum of intertidal environments in Glacier Bay.

Appendix I. Example of field data sheet.

GLACIER BAY INTERTIDAL DATA

LEWIS SHARMAN

SITE #____ DATE___/___'84 LOW TIDE_____m At______ SITE PHOTO #_____

OVERALL SLOPE____% ASPECT______-facing AIR TEMP____°C OTHER PHOTOS____________________

WEATHER______________________________ ____________________

					1.25m										2.5m										3.75m										5m					
SPECIES	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
BARE ROCK																																								
FUCUS DIST.																																								
BAL. BALAN.																																								
BAL. GLAND.																																								
MYTILUS EDUL.																																								
LITT. SITKAN.																																								
NOTOAC. PERS.																																								
NOTOAC. FENE.																																								
COLLIS. PELT.																																								
THAIS LIMA																																								

	SURFACE	2.5m	5m	7.5m
WATER TEMPERATURE (°C)				
SALINITY (o/oo)				
SUSPENDED SEDIMENT (CODE # & ML WATER) MILLIPORE				
GLASS FIBER				

GROUNDED BERGS/100m 0-1m_____ 1-2m_____ 2+m_____

LIGHT PENETRATION (QUANTUM) AIR_____ SURF._____ 1m_____ 2m_____ 3m_____

4m_____ 5m_____ 6m_____ 7m_____ 8m_____

COMMENTS ON REVERSE (INCL. COLLECTION #'S)

Appendix II. 1983 environmental data from two late August through early September sampling dates for six sites. Site F was sampled only on 3 September.

	Site (sampling dates)					
Physical Parameter	A (8-30/ 9-4)	B (8-30/ 9-4)	C (8-30/ 9-4)	D (8-30/ 9-3)	E (8-30/ 9-3)	F (9-3)
Distance from Glacier (km)	1.6	17.1	35.2	49.9	69.9	89.0
Substrate Age (y)	7	41	81	125	164	199
Surface Water Temp. (deg. C)	6/5	6/6.5	10/9	9.5/9	12/13	11
Surface Salinity (o/oo)	9/7	14.5/9	13/20	21/20	28/24	26
Depth of Secchi Disc Disappearance (m)	.8/ .6	.9/ .7	2.1/ 2.0	2.4/ 2.2	2.5/ 2.6	2.7

Appendix III. Environmental data from four depths at 40 sites, with sampling dates and calculated site means. See Appendix IV for suspended particulate data.

Site #	Depth (m)	Distance fr. Glacier (km)	Substrate Age (y)	Air Temp. (°C)	Water Temp. (°C)	Salinity (‰)	Extinc. Coeff.	1% Light Depth (m)	No. Ice Frag. (/100m shoreline)	Slope (%)	Aspect (deg True N)	Sampling Date (d/mo/y)
	0				3.5	8						
	2.5				3.5	14						
1	5				4.0	21						
	7.5				5.0	25						
	Overall Site Mean	0.8	6	7.0	4.0	17.0	2.052	2	624	30	235	7/14/84
	0				6.0	17						
	2.5				5.0	22						
2	5				5.0	22						
	7.5				6.5	25						
	Overall Site Mean	2.4	9	13.5	5.6	21.5	.884	5	2	49	190	8/13/84
	0				6.5	9						
	2.5				4.5	17						
3	5				5.0	22						
	7.5				5.5	25						
	Overall Site Mean	5.0	13	8.0	5.4	18.3	.637	7	0	59	245	7/29/84
	0				9.5	18						
	2.5				6.0	28						
4	5				5.5	30						
	7.5				5.0	31						
	Overall Site Mean	6.2	19	17.0	6.5	26.8	.794	6	0	41	160	6/16/84
	0				5.0	8						
	2.5				5.0	13						
5	5				4.5	14						
	7.5				5.0	26						
	Overall Site Mean	8.7	20	9.0	4.9	15.3	.657	7	11	78	160	6/29/84

Site #	Depth (m)	Distance fr. Glacier (km)	Substrate Age (y)	Air Temp. (°C)	Water Temp. (°C)	Salinity (‰)	Extinc. Coeff.	1% Light Depth (m)	No. Ice Frag. (/100m shoreline)	Slope (%)	Aspect (deg True N)	Sampling Date (d/mo/y)
	0				7.0	15						
	2.5				6.0	15						
6	5				6.5	15						
	7.5				7.0	28						
	Overall Site Mean	9.4	21	16.0	6.6	18.3	.436	11	72	49	185	8/14/84
	0				5.5	12						
	2.5				9.5	19						
7	5				5.0	26						
	7.5				9.5	27						
	Overall Site Mean	11.3	23	11.0	7.4	21.0	1.354	3	106	32	170	6/15/84
	0				6.0	14						
	2.5				5.0	22						
8	5				5.5	28						
	7.5				5.5	29						
	Overall Site Mean	13.3	29	11.5	5.5	23.3	.508	9	0	33	255	7/13/84
	0				6.5	14						
	2.5				5.5	19						
9	5				5.5	22						
	7.5				5.5	27						
	Overall Site Mean	13.7	34	12.0	5.8	20.5	.844	5	0	26	240	7/28/84
	0				6.5	16						
	2.5				6.0	16						
10	5				5.5	24						
	7.5				5.5	26						
	Overall Site Mean	17.8	45	9.5	5.9	20.5	.437	11	0	45	190	7/12/84

Site #	Depth (m)	Distance fr. Glacier (km)	Substrate Age (y)	Air Temp. (°C)	Water Temp. (°C)	Salinity (‰)	Extinc. Coeff.	1% Light Depth (m)	No. Ice Frag. (/100m shoreline)	Slope (%)	Aspect (deg True N)	Sampling Date (d/mo/y)
	0				6.0	19						
	2.5				5.5	21						
11	5				5.5	24						
	7.5				5.5	28						
	Overall Site Mean	19.3	47	13.5	5.6	23.0	.928	5	3	30	105	7/15/84
	0				4.5	8						
	2.5				6.0	22						
12	5				6.0	25						
	7.5				7.0	24						
	Overall Site Mean	20.5	48	8.5	5.9	19.8	.423	11	5	44	275	8/12/84
	0				7.5	16						
	2.5				7.0	28						
13	5				5.0	26						
	7.5				4.5	26						
	Overall Site Mean	22.0	53	11.0	6.0	24.0	.687	7	1	33	250	6/14/84
	0				7.5	18						
	2.5				6.5	27						
14	5				6.0	27						
	7.5				6.5	27						
	Overall Site Mean	23.0	59	13.0	6.6	24.8	.357	13	2	46	180	7/30/84
	0				6.5	12						
	2.5				5.0	22						
15	5				5.0	28						
	7.5				5.5	29						
	Overall Site Mean	24.9	68	10.5	5.5	22.8	.300	15	0	45	205	7/01/84

Site #	Depth (m)	Distance fr. Glacier (km)	Substrate Age (y)	Air Temp. (°C)	Water Temp. (°C)	Salinity (‰)	Extinc. Coeff.	1% Light Depth (m)	No. Ice Frag. (/100m shoreline)	Slope (%)	Aspect (deg True N)	Sampling Date (d/mo/y)
	0				5.0	8						
	2.5				6.0	22						
16	5				7.0	23						
	7.5				7.0	25						
	Overall Site Mean	24.9	68	8.0	6.3	19.5	.467	10	1	52	095	8/11/84
	0				7.5	15						
	2.5				6.5	18						
17	5				6.0	25						
	7.5				6.5	27						
	Overall Site Mean	27.4	77	12.0	6.6	21.3	.317	15	0	28	085	7/16/84
	0				8.5	17						
	2.5				7.0	25						
18	5				7.0	28						
	7.5				7.0	29						
	Overall Site Mean	30.5	79	13.5	7.4	24.8	.560	8	0	33	140	7/31/84
	0				7.5	9						
	2.5				7.5	18						
19	5				7.0	25						
	7.5				5.5	28						
	Overall Site Mean	32.6	80	11.5	6.9	20.0	.411	11	0	55	045	6/28/84
	0				9.0	23						
	2.5				9.0	22						
20	5				9.0	22						
	7.5				8.5	22						
	Overall Site Mean	33.3	80	10.0	8.9	22.3	.558	8	0	50	105	8/26/84

Site #	Depth (m)	Distance fr. Glacier (km)	Substrate Age (y)	Air Temp. (°C)	Water Temp. (°C)	Salinity (‰)	Extinc. Coeff.	1% Light Depth (m)	No. Ice Frag. (/100m shoreline)	Slope (%)	Aspect (deg True N)	Sampling Date (d/mo/y)
	0				7.0	15						
	2.5				7.5	31						
21	5				7.0	31						
	7.5				7.0	30						
	Overall Site Mean	33.8	80	14.5	7.1	26.8	.462	10	0	65	305	6/18/84
	0				6.0	9						
	2.5				7.0	20						
22	5				7.5	22						
	7.5				7.5	25						
	Overall Site Mean	34.5	80	8.5	7.0	19.0	.815	6	0	35	135	8/10/84
	0				9.5	13						
	2.5				8.5	24						
23	5				8.0	24						
	7.5				8.0	27						
	Overall Site Mean	35.1	81	12.5	8.5	22.0	.552	8	0	37	255	7/27/84
	0				7.5	15						
	2.5				8.0	24						
24	5				7.5	24						
	7.5				6.5	27						
	Overall Site Mean	35.6	82	10.5	7.4	22.5	.382	12	0	57	245	7/10/84
	0				8.0	24						
	2.5				7.0	29						
25	5				7.5	31						
	7.5				7.0	31						
	Overall Site Mean	37.2	83	14.0	7.4	28.8	.194	24	0	83	290	6/13/84

Site #	Depth (m)	Distance fr. Glacier (km)	Substrate Age (y)	Air Temp. (°C)	Water Temp. (°C)	Salinity (‰)	Extinc. Coeff.	1% Light Depth (m)	No. Ice Frag. (/100m shoreline)	Slope (%)	Aspect (deg True N)	Sampling Date (d/mo/y)
26	0				8.0	24						
	2.5				7.5	22						
	5				7.5	25						
	7.5				8.0	27						
	Overall Site Mean	45.0	114	11.5	7.8	24.5	.277	17	0	39	025	7/02/84
27	0				8.5	21						
	2.5				9.0	20						
	5				9.0	26						
	7.5				9.0	27						
	Overall Site Mean	47.3	119	12.0	8.9	23.5	.327	14	0	70	250	8/09/84
28	0				9.5	22						
	2.5				10.0	23						
	5				10.5	24						
	7.5				9.0	26						
	Overall Site Mean	48.7	123	9.5	9.8	23.8	.224	21	0	16	250	7/09/84
29	0				9.0	26						
	2.5				8.5	26						
	5				8.5	26						
	7.5				8.0	30						
	Overall Site Mean	48.7	123	14.0	8.5	27.0	.356	13	0	36	080	6/27/84
30	0				12.0	29						
	2.5				10.0	26						
	5				9.5	28						
	7.5				9.0	30						
	Overall Site Mean	50.7	126	13.0	10.1	28.3	.378	12	0	53	275	7/26/84

Site #	Depth (m)	Distance fr. Glacier (km)	Substrate Age (y)	Air Temp. (°C)	Water Temp. (°C)	Salinity (‰)
	0				11.5	28
	2.5				10.5	28
31	5				9.0	31
	7.5				9.0	30
	Overall Site Mean	52.1	126	17.0	10.0	29.3
	0				9.0	30
	2.5				8.0	29
32	5				7.5	29
	7.5				7.5	29
	Overall Site Mean	52.4	126	14.0	8.0	29.3
	0				11.0	26
	2.5				10.5	26
33	5				9.5	28
	7.5				9.0	30
	Overall Site Mean	57.1	135	13.5	10.0	27.5
	0				11.0	24
	2.5				9.0	26
34	5				8.5	27
	7.5				8.5	28
	Overall Site Mean	57.9	135	15.5	9.3	26.3
	0				10.5	21
	2.5				9.0	27
35	5				8.5	28
	7.5				8.0	28
	Overall Site Mean	59.0	139	11.0	9.0	26.0

Extinc. Coeff.	1% Light Depth (m)	No. Ice Frag. (/100m shoreline)	Slope (%)	Aspect (deg True N)	Sampling Date (d/mo/y)
.311	15	0	49	055	7/17/84
.192	24	0	85	230	6/12/84
.330	14	0	46	260	7/25/84
.284	16	0	54	075	8/01/84
.400	12	0	22	260	7/08/84

Site #	Depth (m)	Distance fr. Glacier (km)	Substrate Age (y)	Air Temp. (°C)	Water Temp. (°C)	Salinity (‰)
	0				12.0	25
	2.5				10.0	24
36	5				9.0	26
	7.5				9.0	26
	Overall Site Mean	61.1	143	15.5	10.0	25.3
	0				11.0	26
	2.5				9.5	26
37	5				9.0	26
	7.5				9.0	28
	Overall Site Mean	63.5	149	15.0	9.6	26.5
	0				10.0	24
	2.5				9.0	30
38	5				8.5	30
	7.5				9.0	30
	Overall Site Mean	64.5	154	14.0	9.1	28.5
	0				10.5	25
	2.5				9.5	25
39	5				9.5	25
	7.5				9.5	26
	Overall Site Mean	68.4	161	12.0	9.8	25.3
	0				9.5	30
	2.5				8.5	31
40	5				8.5	31
	7.5				8.5	30
	Overall Site Mean	80.4	184	15.0	8.8	30.5

Extinc. Coeff.	1% Light Depth (m)	No. Ice Frag. (/100m shoreline)	Slope (%)	Aspect (deg True N)	Sampling Date (d/mo/y)
.413	11	0	44	050	8/02/84
.355	13	0	38	050	8/03/84
.228	20	0	31	290	6/11/84
.267	17	0	55	060	6/26/84
.212	22	0	65	045	6/24/84

Appendix IV. Suspended particulate data from four depths at 26 sites (40 sites for total suspended particulate concentration in seawater), with calculated site means.

SITE #	DEPTH (m)	PC (mg/L)	PN (mg/L)	C:N	TOT. SUSP. PARTIC. (mg/L)	PC: TOT. SUSP. PARTIC. (% wt.)	PN: TOT. SUSP. PARTIC. (% wt.)
1	0	1.00	.11	9.1	42	2.38	.26
	2.5	1.16	.09	12.5	70	1.66	.13
	5	1.82	.06	32.1	167	1.09	.04
	7.5	5.03	.05	100.5	358	1.41	.01
OVERALL SITE MEAN		2.25	.08	38.6	159	1.64	.11
2	0	2.84	.08	34.1	153	1.86	.05
	2.5	1.36	.04	37.0	107	1.27	.04
	5	.69	.03	23.0	37	1.86	.08
	7.5	.37	.02	18.7	30	1.23	.07
OVERALL SITE MEAN		1.32	.04	28.2	82	1.56	.06
3	0	.14	.02	6.8	13	1.08	.15
	2.5	.47	.12	4.1	17	2.76	.71
	5	.38	.10	3.8	17	2.24	.59
	7.5	.11	.02	4.9	13	.85	.15
OVERALL SITE MEAN		.28	.07	4.9	15	1.73	.40
4	0				43		
	2.5				43		
	5				40		
	7.5				37		
OVERALL SITE MEAN					41		
5	0				20		
	2.5				17		
	5				20		
	7.5				33		
OVERALL SITE MEAN					23		
6	0	.27	.02	11.6	30	.90	.07
	2.5	.27	.03	10.0	17	1.59	.18
	5	.17	.03	6.4	17	1.00	.18
	7.5	.31	.02	13.1	15	2.07	.13
OVERALL SITE MEAN		.26	.03	10.3	20	1.39	.14

SITE #	DEPTH (m)	PC (mg/L)	PN (mg/L)	C:N	TOT. SUSP. PARTIC. (mg/L)	PC: TOT. SUSP. PARTIC. (% wt.)	PN: TOT. SUSP. PARTIC. (% wt.)
7	0				30		
	2.5				87		
	5				40		
	7.5				27		
OVERALL SITE MEAN					46		
8	0	.98	.18	5.5	27	3.63	.67
	2.5	.47	.05	9.3	27	1.74	.19
	5	-	.01	-	23	-	.04
	7.5	-	.01	-	23	-	.04
OVERALL SITE MEAN		.36	.06	7.4	25	2.69	.24
9	0	.51	.06	8.0	27	1.89	.22
	2.5	1.51	.17	8.7	27	5.59	.63
	5	1.15	.19	5.9	27	4.26	.70
	7.5	.17	.03	5.0	20	.85	.15
OVERALL SITE MEAN		.84	.11	6.9	25	3.15	.43
10	0	.27	.03	8.9	19	1.42	.16
	2.5	.28	.05	5.5	17	1.65	.29
	5	.10	.02	4.4	22	.45	.09
	7.5	.02	.01	1.5	17	.12	.06
OVERALL SITE MEAN		.17	.03	5.1	19	.91	.15
11	0	.73	.05	14.5	30	2.43	.17
	2.5	.32	.03	9.5	33	.97	.09
	5	.41	.02	20.7	43	.95	.05
	7.5	.44	.03	16.5	23	1.91	.13
OVERALL SITE MEAN		.48	.03	15.3	32	1.57	.11
12	0	.28	.03	10.7	14	2.00	.21
	2.5	.20	.04	4.7	14	1.43	.29
	5	.18	.04	4.2	12	1.50	.33
	7.5	.17	.03	5.4	10	1.70	.30
OVERALL SITE MEAN		.21	.04	6.3	13	1.66	.28

SITE #	DEPTH (m)	PC (mg/L)	PN (mg/L)	C:N	TOT. SUSP. PARTIC. (mg/L)	PC: TOT. SUSP. PARTIC. (% wt.)	PN: TOT. SUSP. PARTIC. (% wt.)
13	0				52		
	2.5				27		
	5				17		
	7.5				7		
OVERALL SITE MEAN					26		
14	0	.66	.06	11.1	12	5.50	.50
	2.5	.63	.07	9.6	12	5.25	.58
	5	.19	.03	5.5	12	1.58	.25
	7.5	.18	.03	5.6	12	1.50	.25
OVERALL SITE MEAN		.42	.05	8.0	12	3.46	.40
15	0				8		
	2.5				12		
	5				8		
	7.5				10		
OVERALL SITE MEAN					10		
16	0	.29	.03	9.1	8	3.63	.38
	2.5	.26	.05	5.5	12	2.17	.42
	5	.22	.05	4.4	12	1.83	.42
	7.5	.19	.05	4.2	10	1.90	.50
OVERALL SITE MEAN		.24	.05	5.8	11	2.38	.43
17	0	.70	.10	7.0	20	3.50	.50
	2.5	.24	.03	7.1	10	2.40	.30
	5	.42	.06	6.6	12	3.50	.50
	7.5	.29	.04	7.2	10	2.90	.40
OVERALL SITE MEAN		.41	.06	7.0	13	3.08	.43
18	0	.55	.06	8.8	16	3.44	.38
	2.5	1.32	.16	8.2	20	6.60	.80
	5	.42	.08	5.0	12	3.50	.67
	7.5	.20	.04	4.5	10	2.00	.40
OVERALL SITE MEAN		.62	.09	6.6	15	3.89	.56

SITE #	DEPTH (m)	PC (mg/L)	PN (mg/L)	C:N	TOT. SUSP. PARTIC. (mg/L)	PC: TOT. SUSP. PARTIC. (% wt.)	PN: TOT. SUSP. PARTIC. (% wt.)
19	0				12		
	2.5				6		
	5				10		
	7.5				12		
OVERALL SITE MEAN					10		
20	0	.43	.07	6.4	24	1.79	.29
	2.5	.43	.08	5.4	22	1.95	.36
	5	.50	.08	6.6	22	2.27	.36
	7.5	.43	.06	7.4	22	1.95	.27
OVERALL SITE MEAN		.45	.07	6.5	23	1.99	.32
21	0				16		
	2.5				12		
	5				18		
	7.5				14		
OVERALL SITE MEAN					15		
22	0	.39	.07	6.0	8	4.88	.88
	2.5	.68	.10	6.7	16	4.25	.63
	5	.26	.04	7.2	26	1.00	.15
	7.5	.38	.03	11.8	24	1.58	.13
OVERALL SITE MEAN		.43	.06	7.9	19	2.93	.45
23	0	.63	.07	8.5	20	3.15	.35
	2.5	.95	.13	7.1	16	5.94	.81
	5	.88	.14	6.1	18	4.89	.78
	7.5	.47	.07	6.9	16	2.94	.44
OVERALL SITE MEAN		.73	.10	7.2	18	4.23	.60
24	0	.74	.12	6.3	14	5.29	.86
	2.5	.35	.07	4.8	14	2.50	.50
	5	.20	.05	4.4	12	1.67	.42
	7.5	.21	.05	4.5	10	2.10	.50
OVERALL SITE MEAN		.38	.07	5.0	13	2.89	.57

SITE #	DEPTH (m)	PC (mg/L)	PN (mg/L)	C:N	TOT. SUSP. PARTIC. (mg/L)	PC: TOT. SUSP. PARTIC. (% wt.)	PN: TOT. SUSP. PARTIC. (% wt.)
25	0				20		
	2.5				24		
	5				16		
	7.5				22		
OVERALL SITE MEAN					21		
26	0				18		
	2.5				18		
	5				16		
	7.5				16		
OVERALL SITE MEAN					17		
27	0	.36	.08	4.7	14	2.57	.57
	2.5	.41	.08	5.2	10	4.10	.80
	5	.29	.07	4.1	12	2.42	.58
	7.5	.33	.07	4.6	12	2.75	.58
OVERALL SITE MEAN		.35	.08	4.7	12	2.96	.63
28	0	.52	.10	5.2	12	4.33	.83
	2.5	.57	.13	4.5	12	4.75	1.08
	5	.37	.08	4.7	12	3.08	.67
	7.5	.57	.08	6.7	12	4.75	.67
OVERALL SITE MEAN		.51	.10	5.3	12	4.23	.81
29	0				17		
	2.5				17		
	5				16		
	7.5				17		
OVERALL SITE MEAN					17		
30	0	.51	.08	6.8	16	3.19	.50
	2.5	.74	.11	6.7	16	4.63	.69
	5	.56	.11	5.2	18	3.11	.61
	7.5	.21	.04	5.8	18	1.17	.22
OVERALL SITE MEAN		.51	.09	6.1	17	3.03	.51

SITE #	DEPTH (m)	PC (mg/L)	PN (mg/L)	C:N	TOT. SUSP. PARTIC. (mg/L)	PC: TOT. SUSP. PARTIC. (% wt.)	PN: TOT. SUSP. PARTIC. (% wt.)
31	0	.29	.04	6.6	16	1.81	.25
	2.5	.34	.06	5.4	14	2.43	.43
	5	.28	.05	5.4	16	1.75	.31
	7.5	.31	.06	5.2	14	2.21	.43
OVERALL SITE MEAN		.31	.05	5.7	15	2.05	.36
32	0				22		
	2.5				16		
	5				16		
	7.5				18		
OVERALL SITE MEAN					18		
33	0	.68	.12	5.7	19	3.58	.63
	2.5	.72	.15	4.9	17	4.24	.88
	5	.49	.09	5.2	18	2.72	.50
	7.5	.29	.06	4.8	18	1.61	.33
OVERALL SITE MEAN		.55	.11	5.2	18	3.04	.59
34	0	.43	.08	5.3	12	3.58	.67
	2.5	.51	.11	4.8	14	3.64	.79
	5	.57	.06	8.9	14	4.07	.43
	7.5	.38	.07	5.5	14	2.71	.50
OVERALL SITE MEAN		.47	.08	6.1	14	3.50	.60
35	0	.43	.07	6.1	18	2.39	.39
	2.5	.41	.08	5.2	16	2.56	.50
	5	.46	.09	5.3	16	2.88	.56
	7.5	.35	.07	4.8	14	2.50	.50
OVERALL SITE MEAN		.41	.08	5.4	16	2.58	.49
36	0	.31	.07	4.6	14	2.21	.50
	2.5	.40	.06	6.5	14	2.86	.43
	5	.52	.07	7.1	12	4.33	.58
	7.5	.47	.07	6.4	14	3.36	.50
OVERALL SITE MEAN		.43	.07	6.2	14	3.19	.50

SITE #	DEPTH (m)	PC (mg/L)	PN (mg/L)	C:N	TOT. SUSP. PARTIC. (mg/L)	PC: TOT. SUSP. PARTIC. (% wt.)	PN: TOT. SUSP. PARTIC. (% wt.)
37	0	.46	.07	7.0	16	2.88	.44
	2.5	.66	.10	6.5	14	4.71	.71
	5	.78	.11	7.0	16	4.88	.69
	7.5	.49	.07	6.6	12	4.08	.58
OVERALL SITE MEAN		.60	.09	6.8	15	4.14	.61
38	0				16		
	2.5				14		
	5				16		
	7.5				20		
OVERALL SITE MEAN					17		
39	0				18		
	2.5				20		
	5				18		
	7.5				16		
OVERALL SITE MEAN					18		
40	0				18		
	2.5				17		
	5				19		
	7.5				20		
OVERALL SITE MEAN					19		

Appendix V. Results from 1984 dowel experiment. Site locations (A-F) were the same as for 1983 study sites (Fig. 3).

Site	Vertical Intertidal Level (+m MLLW)	No. Dowels Placed Early Summer (Date = d/mo/y)		No. Dowels Still In Place Late Summer (Date = d/mo/y)	
	2		10		0
A	3.5	(5/31/84)	10	(8/29/84)	0
	5		10		2
	Total		30		2
	2		10		9
B	3.5	(5/30/84)	10	(8/27/84)	8
	5		10		10
	Total		30		27
	2		10		8
C	3.5	(5/28/84)	10	(8/26/84)	8
	5		10		3
	Total		30		19
	2		10		10
D	3.5	(5/27/84)	10	(8/23/84)	10
	5		10		10
	Total		30		30
	2		10		8
E	3.5	(5/25/84)	10	(8/22/84)	9
	5		10		7
	Total		30		24
	2		10		*
F	3.5	(5/23/84)	10	(8/21/84)	6
	5		10		8
	Total		30		14

* Could not relocate dowel set.

Appendix VI. List of intertidal species encountered at each site for five vertical intertidal levels (0 m MLLW level was sampled for 30 of the 40 sites). Frequency of occurrence, mean percent coverage or abundance (number of individuals per 0.1 m^2), and standard error are listed for each species (see Table 3 for meanings of abbreviated species names) and for percent total unoccupied substrate surface and species richness (number of species per quadrat). n = 10 for each intertidal level at a site. Abundance was recorded for all molluscs except *Mytilus edulis*, all crustaceans except *Balanus* spp., and all anemones, nemerteans, echinoderms, and fishes. Percent coverage was recorded for all other animal species and for all algae. Coverages < 1% were assigned a value of 0.1%. "*" beside a site number indicates that the 0 m MLLW level was not sampled.

	0m MLLW			1.25m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Myed	90	2.02	.59	70	.62	.22
Basp	90	12.30	4.03	80	1.92	.79
Ensp	70	.26	.19	100	1.63	.59
Brsl	100	85.50	3.83	100	47.80	4.94
Total Unoccupied Surface	0	0	0	100	48.7	5.62
Species Richness	100	3.5	.31	100	3.5	.22

Site # 1								
2.5m MLLW			3.75m MLLW			5m MLLW		
Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
10	.60	.60						
100	19.20	3.33	70	5.80	1.90			
100	17.50	3.30						
100	75.2	4.41	100	94.2	1.90	100	100.0	0
100	2.1	.10	70	.7	.15	0	0	0

Site # 2

	0m MLLW			1.25m MLLW			2.5m MLLW	
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean
Myed	90	6.80	2.71	70	3.73	2.95	40	.13
Cosp	60	.70	.21	10	.50	.50		
Basp	100	16.00	3.19	100	13.81	4.12	100	18.40
Bast	90	.18	.09	60	.06	.02	60	.06
Amsp				10	.40	.40		
Ulsp				30	.12	.10	80	4.31
Ensp								
Fudi				20	4.70	3.98	90	2.04
Total Unoccupied Surface	100	77.5	5.60	100	81.1	6.68	100	75.9
Species Richness	100	2.5	.22	100	2.4	.34	100	3.1

	3.75m MLLW			5m MLLW		
S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
.10						
3.91	100	6.31	2.27	40	.53	.50
.02	20	.02	.01			
1.56	100	54.50	5.95			
				70	3.93	2.93
1.01	80	.85	.59	10	.01	.01
3.98	100	39.4	5.91	100	96.1	2.94
.23	100	2.8	.13	70	1.2	.33

	0m MLLW			1.25m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Myed	100	26.00	3.80	100	8.01	1.75
Hiar	20	.80	.61			
Cosp	90	3.00	.61	40	.40	.16
Basp	100	17.70	3.19	100	18.70	4.07
Bast	60	.06	.02	70	.07	.02
Amsp						
Uusp						
Ensp	20	.02	.01	40	.04	.02
Grsl						
Fudi				40	1.41	.86
Brfi						
Posp				40	.43	.40
Total Unoccupied Surface	100	53.3	5.79	100	71.3	5.37
Species Richness	100	3.3	.26	100	3.6	.37

Site # 3								
2.5m MLLW			3.75m MLLW			5m MLLW		
Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
60	2.34	1.46	10	.01	.01			
10	.10	.10						
90	22.00	3.43	100	10.60	2.84			
70	.07	.02	80	.08	.01			
40	.90	.43						
10	.10	.10						
100	.37	.14	100	6.60	1.70	20	.02	.01
			10	1.00	1.00			
100	12.01	1.87	70	1.32	.53			
50	1.30	.54	10	.01	.01			
100	65.8	3.72	100	81.1	3.81	100	100.0	0
100	4.9	.38	100	2.9	.28	20	.2	.13

Site # 4															
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Myed	100	43.60	9.14	100	39.60	9.13	100	6.50	1.25	60	.06	.02			
Hiar	20	.20	.13	10	.10	.10									
Cosp	100	13.30	4.58	90	10.50	3.90	100	34.70	10.05	10	.10	.10			
Basp	100	4.90	.81	100	24.90	4.95	100	28.20	3.37	100	6.81	1.52			
Bast	70	.07	.02	80	.08	.01	80	1.23	.53	80	.08	.01			
Amsp				20	.50	.34	50	.90	.38	50	2.10	1.06			
Gnor				10	.10	.10	40	.40	.16	40	.70	.34			
Ulsp				20	.02	.01									
Ensp				10	.10	.10	50	.42	.22	20	.11	.10			
Fudi	100	1.44	.68	80	12.70	3.14	100	45.10	6.24	100	54.40	11.51			
Brfi	40	.22	.13	70	3.40	.98	70	6.80	2.03	60	8.50	3.73			
Total Unoccupied Surface	100	50.8	8.92	100	28.5	8.69	100	42.70	4.66	100	42.0	11.38	100	100.0	0
Species Richness	100	4.6	.16	100	5.1	.43	100	6.1	.28	100	4.4	.45	0	0	0

	Site # 5*														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Myed				100	39.00	6.70									
Cosp				60	7.90	2.89	10	.30	.30						
Basp				100	30.80	4.47	100	29.20	6.30	100	17.30	3.60			
Bast				10	.01	.01	80	.08	.01	30	.03	.02			
Gnor				10	.10	.10				10	.10	.10			
Amsp							20	.60	.50						
Ensp							70	.43	.16	90	2.20	.68			
Grsl				50	2.11	1.05	30	.51	.34						
Fudi							90	17.82	6.36	80	4.00	.95			
Brfi				30	.31	.21	20	.21	.20						
Total Unoccupied Surface				100	28.2	4.15	100	49.8	8.15	100	78.2	3.89	100	100.0	0
Species Richness				100	3.5	.37	100	4.2	.39	100	2.8	.25	0	0	0

	Site # 6														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Myed	100	26.70	6.34	100	24.10	5.72	100	5.12	1.42	10	.01	.01			
Cosp	100	5.80	.80	100	16.50	2.70	90	8.20	1.70	50	1.00	.37			
Basp	100	28.50	3.88	100	11.40	2.23	100	14.71	3.85	100	3.61	.66			
Bast	50	.05	.02	80	.08	.01	90	.09	.01	40	.04	.02			
Amsp				10	.10	.10									
Uusp							10	.01	.01	10	.20	.20	10	.10	.10
Ensp							90	.95	.58	100	12.60	3.42	10	.01	.01
Fudi	10	.01	.01	60	5.22	3.46	100	25.31	8.42	100	56.00	4.76			
Brfi				30	.71	.52	40	1.51	.76	50	2.00	.84			
Posp				10	.01	.01	10	.20	.20						
Total Unoccupied Surface	100	45.8	5.18	100	63.5	5.03	100	57.3	6.55	100	37.0	5.44	100	99.9	.10
Species Richness	100	3.1	.10	100	4.1	.38	100	5.4	.27	100	4.2	.33	20	.2	.13

	Site # 7														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Myed	60	3.32	2.01	90	24.00	4.76	20	.40	.31	20	.02	.01			
Hiar	10	.10	.10												
Cosp	30	1.40	.79	100	11.20	2.48				10	.10	.10			
Basp	60	3.11	1.18	100	19.00	3.06	100	15.52	4.10	90	11.61	3.97			
Bast	70	.16	.09	70	.07	.02	100	.19	.09	50	.05	.02			
Amsp							50	2.10	.87	40	1.70	1.00			
Uusp													30	1.10	.66
Ensp										40	.70	.34	10	.60	.60
Fudi				10	.01	.01	100	38.50	8.10	100	38.01	8.79	10	.10	.10
Brfi										10	1.00	1.00			
Total Unoccupied Surface	100	94.0	2.64	100	56.0	6.53	100	56.0	7.22	100	54.3	8.26	100	98.2	.87
Species Richness	80	1.8	.42	100	3.1	.23	100	2.7	.21	100	3.1	.43	40	.5	.22

	Site # 8														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Myed	100	28.00	3.18	80	12.30	4.06	100	10.91	3.80	100	4.51	2.31			
Cosp	100	16.40	2.66	90	16.60	3.08	90	14.60	4.15	100	13.10	2.99			
Lisi				100	20.60	4.90	100	109.50	40.92	100	153.40	40.14			
Basp	100	24.81	6.44	100	13.60	3.37	100	20.70	2.85	100	18.80	2.69			
Bast	40	.04	.02	90	.09	.01	90	.09	.01	90	.09	.01			
Amsp										20	.20	.20			
Gnor										10	.10	.10			
Ulsp	30	.12	.10	40	.04	.02									
Ensp							60	.06	.02	70	1.11	.34	20	.02	.01
Grsl							10	.30	.30						
Fudi	90	4.11	1.98	50	.14	.10	90	12.61	4.86	100	55.50	6.81			
Brfi	20	3.00	2.13				40	1.80	1.04						
Posp	40	1.61	1.05	50	4.40	2.16	60	.72	.33						
Lisp	10	.10	.10												
Total Unoccupied Surface	100	45.4	7.66	100	72.7	5.40	100	60.4	6.97	100	32.2	6.33	100	100.0	0
Species Richness	100	4.9	.35	100	5.1	.28	100	6.5	.50	100	5.9	.23	20	.2	.13

	0m MLLW			1.25m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Nesp						
Myed	100	43.90	8.53	100	23.40	5.33
Hiar	100	20.50	5.84			
Cosp	100	13.90	1.87	100	39.30	9.33
Lisi				50	1.60	.65
Basp	100	20.60	7.95	100	10.81	2.77
Bast	50	.05	.02	80	.08	.01
Acsp	10	.01	.01			
Ulsp	10	.20	.20			
Ensp				20	.02	.01
Grsl						
Fudi	10	.01	.01	20	.02	.01
Mein	20	.31	.30			
Alte	10	.01	.01			
Brfi						
Posp	50	.14	.10	40	.82	.69
Total Unoccupied Surface	100	35.6	8.46	100	65.0	7.60
Species Richness	100	5.1	.43	100	4.3	.40

Site # 9

2.5m MLLW			3.75m MLLW			5m MLLW		
Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
			10	.20	.20			
100	17.30	2.97	90	4.30	1.08			
100	8.10	2.15	70	3.10	.90			
100	78.20	16.75	100	94.50	16.17	20	.50	.34
100	34.00	3.93	100	26.50	3.50	50	.62	.34
100	.10	0	100	.19	.09	10	.01	.01
100	.38	.20	90	.74	.25	40	.13	.10
40	2.70	1.51						
100	12.12	4.41	100	76.00	6.66	50	1.93	1.50
20	.30	.21	20	.60	.50			
80	.92	.31	10	.20	.20			
100	45.5	5.45	100	20.0	5.32	100	97.4	1.72
100	7.4	.16	100	5.9	.28	70	1.6	.48

	0m MLLW			1.25m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Myed	100	54.00	7.30	100	53.50	6.83
Hiar	10	.10	.10			
Cosp	100	24.60	4.14	100	24.00	3.23
Lisi				90	21.00	6.72
Basp	20	.02	.01	100	18.01	3.26
Bast	10	.01	.01	80	.08	.01
Grsl	20	.40	.27			
Fudi	30	.31	.21	20	.02	.01
Mein	10	.20	.20			
Posp	20	.02	.01			
Lisp	40	.04	.02	10	.01	.01
Total Unoccupied Surface	100	46.0	7.30	100	29.5	3.61
Species Richness	100	3.5	.31	100	4.2	.13

Site # 10								
2.5m MLLW			3.75m MLLW			5m MLLW		
Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
100	27.00	4.73	70	2.82	1.49			
100	9.00	2.33	50	4.00	1.53			
100	495.80	116.48	100	484.80	196.15	90	9.10	3.00
100	58.50	5.27	100	26.10	6.40			
80	.08	.01	80	.08	.01			
20	.02	.01	100	26.22	9.69			
90	14.5	3.53	100	51.7	10.06	100	100.0	0
100	4.2	.13	100	4.2	.25	90	.9	.10

								Site # 11
		0m MLLW			1.25m MLLW			2.5m MLLW
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean
Myed	100	41.40	5.01	100	43.40	9.85	100	2[illegible].60
Hiar	70	3.00	1.30	10	.10	.10		
Cosp	100	37.50	4.15	100	56.80	11.77	100	21.30
Lisi				90	16.20	4.03	100	238.20
Pasp	100	7.00	1.94	100	24.20	5.79	100	38.00
Bast	50	.05	.02	100	.01	0	80	.08
Amsp								
Gnor				10	.20	.20	10	.10
Uusp	10	.01	.01					
Ensp							20	.02
Grsl				30	.03	.02		
Fudi	80	1.02	.79	20	.21	.20	40	.04
Brfi								
Brsl				10	.01	.01	60	.06
Fosp	10	.01	.01					
Total Unoccupied Surface	100	52.0	3.97	100	3[illegible].4	5.73	100	37.0
Species Richness	100	4.7	.30	100	4.7	.21	100	5.3

	3.75m MLLW			5m MLLW		
S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
6.47	100	5.31	1.42			
3.44	100	36.40	9.61			
37.29	100	313.00	54.67	100	34.00	11.47
6.71	100	17.70	3.64	20	.11	.10
.01	80	.35	.14			
	10	.20	.20			
.10						
.01	50	.14	.10			
.02	100	41.50	7.85	40	.82	.55
	10	.50	.50			
.02	10	.01	.01			
8.21	100	37.6	5.04	100	99.1	.64
.26	100	5.8	.20	100	1.6	.27

	0m MLLW			1.25m MLLW			Fr
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Fr
Myed	100	79.50	3.91	100	67.00	4.61	
Hiar	60	1.20	.42	10	.10	.10	
Cosp	100	45.40	8.16	100	63.60	10.61	
Lisi	10	.10	.10	90	3.90	1.07	
Basp	90	1.65	.74	100	3.93	1.41	
Bast	50	.05	.02	40	.04	.02	
Ulsp	10	.01	.01				
Ensp							
Fudi	10	.01	.01	10	.01	.01	
Lisp	20	.02	.01				
Total Unoccupied Surface	100	18.0	3.18	100	30.0	4.08	
Species Richness	100	4.1	.31	100	4.1	.18	

Site # 12								
2.5m MLLW			3.75m MLLW			5m MLLW		
req.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
100	47.50	2.61	100	7.12	2.45			
100	69.80	12.75	100	46.90	10.46			
100	215.00	67.40	100	245.00	46.12	40	.70	.40
100	40.00	2.98	100	37.00	4.23			
100	.10	0	90	3.11	.69			
10	.01	.01						
10	.01	.01				70	2.12	.76
60	14.02	5.76	90	16.90	5.49	50	.43	.30
100	12.5	3.18	100	42.5	3.27	100	97.5	.95
100	4.8	.20	100	4.9	.10	70	1.6	.40

	Site # 13														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Myed	100	82.30	6.84	100	80.60	5.04	90	26.80	9.17	60	1.52	.82			
Hiar	50	1.00	.37	10	.10	.10									
Cosp	100	54.00	9.68	100	56.00	10.67	100	30.90	8.36	90	18.00	7.50			
Lisi				60	18.20	8.09	100	275.00	51.84	90	243.00	46.55	100	124.00	31.24
Basp	50	.33	.21	100	6.22	2.12	100	55.60	9.96	100	10.00	6.18			
Bast	70	.07	.02	70	.94	.54	90	1.80	.29	60	.54	.34			
Gnor							20	.20	.13	20	.20	.13			
Acsp				10	.10	.10	10	.01	.01				10	.01	.01
Ensp													10	.01	.01
Fudi	50	.05	.02	60	.24	.13	40	.32	.21	100	73.30	7.90	40	1.22	1.00
Alte	10	.10	.10												
Posp	20	.02	.01	20	.21	.20									
Total Unoccupied Surface	90	17.5	6.86	100	12.8	3.58	100	16.8	3.80	100	19.2	4.64	100	98.8	1.00
Species Richness	100	4.1	.31	100	4.6	.37	100	4.6	.22	100	4.5	.34	100	1.6	.27

	Site # 14														
	0m MLLW			1.75m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Nesp	20	.20	.13	10	.10	.10									
Myed	100	51.50	5.22	100	48.70	8.59	100	39.00	7.37	100	13.71	3.57			
Hiar	70	2.70	.83	10	.10	.10									
Cosp	100	9.30	1.42	100	48.30	7.03	100	29.60	4.92	100	18.00	3.31			
Lisi	30	.60	.34	50	3.50	1.84	100	370.00	77.07	100	305.00	62.10	100	24.80	4.01
Basp	100	1.13	.30	100	2.32	.64	100	45.30	5.83	100	43.90	3.56	10	.01	.01
Bast	50	.95	.02	80	.08	.01	100	.10	0	50	.55	.15			
Ulsp	10	.01	.01												
Ensp	30	.03	.02							20	.02	.01	10	.01	.01
Fudi	50	.92	.52	30	.03	.02	80	10.41	4.13	80	8.22	3.23	60	.64	.49
Fosp	30	.03	.02				20	.02	.01						
Total Unoccupied Surface	100	46.9	5.58	90	49.3	8.11	100	14.7	5.98	100	41.5	4.72	100	99.4	.50
Species Richness	100	5.4	.31	100	3.9	.23	100	5.0	.21	100	5.0	.21	100	1.8	.20

	Site # 15														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Nesp	10	.10	.10												
Myed	100	75.10	6.68	100	91.50	2.69	100	8.91	2.05	50	.05	.02			
Hiar	40	.40	.16												
Cosp	100	16.60	1.89	100	13.40	2.47	100	8.00	1.73	90	3.10	.74			
Nope										50	1.60	.75			
Lisi				100	10.50	4.44	100	667.00	70.32	100	455.00	76.00	100	16.50	4.60
Masp	60	.24	.13	100	3.64	1.29	100	82.00	3.35	100	8.10	1.73			
Past	40	.04	.02	40	.04	.02	100	.19	.09	90	.18	.09			
Gnor				10	.10	.10									
Ulsp	60	.15	.10							20	.11	.10			
Ensp	30	.03	.02	10	.01	.01	40	.04	.02	10	.01	.01	10	.01	.01
Gesl	20	.51	.50												
Fudi	10	.01	.01	60	1.92	.96	90	22.30	4.78	100	59.50	9.96			
Brfi							10	.01	.01						
Posp	70	.84	.51	50	.82	.51									
Total Unoccupied Surface	100	24.4	6.27	40	3.5	2.00	100	6.8	.89	100	36.3	9.01	100	100.0	0
Species Richness	100	5.1	.46	100	5.3	.30	100	5.4	.22	100	5.2	.36	100	1.1	.10

	Site # 16														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Myed	100	56.70	10.08	100	37.00	5.59	100	49.00	4.33	100	10.71	2.43	10	.01	.01
Cosp	100	37.10	2.62	100	58.90	7.57	100	33.60	7.01	100	27.90	6.63			
Lisi	30	.30	.15	100	8.60	1.21	100	182.20	34.05	100	218.50	36.33	100	25.20	7.88
Basp	30	.03	.02	100	1.81	.35	100	32.50	2.39	100	35.00	6.32	60	.25	.20
Bast	40	.04	.02	100	.10	0	90	.28	.19	90	.27	.12	10	.01	.01
Ulsp	20	.02	.01	20	.11	.10	20	.02	.01						
Fudi	50	.53	.34	10	.01	.01	10	.40	.40	100	42.00	7.75	80	3.21	1.21
Total Unoccupied Surface	100	43.2	10.30	100	61.8	5.45	100	21.1	4.01	100	31.0	4.76	100	96.6	1.34
Species Richness	100	3.6	.34	100	4.3	.15	100	4.3	.15	100	5.0	0	100	2.5	.31

	0m MLLW			1.25m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Nesp						
Myed	100	70.00	6.41	100	70.00	6.54
Hiar	30	1.00	.56			
Cosp	100	37.30	5.44	100	22.00	3.58
Nope						
Lisi	20	.60	.50	100	8.30	2.28
Dasp	60	.34	.21	80	9.11	2.99
Bast	50	.05	.02	30	.03	.02
Amsp						
Acsp	10	.01	.01	50	.71	.30
Ulsp	100	5.60	1.19	90	2.81	.77
Ensp						
Fudi	10	.01	.01	40	1.40	.72
Mein				10	.01	.01
Brfi						
Posp				20	.31	.30
Ppsp	60	2.00	.76	100	2.23	.78
Lisp	50	.05	.02			
Total Unoccupied Surface	100	28.8	6.12	100	16.1	3.74
Species Richness	100	5.5	.43	100	6.9	.31

Site # 17

2.5m MLLW			3.75m MLLW			5m MLLW		
Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
20	.20	.13						
100	28.50	2.89	50	.63	.50			
100	24.50	3.27	80	6.30	2.10			
			20	.80	.61			
100	507.00	93.00	100	194.10	49.17	80	30.90	14.12
100	57.50	4.61	100	21.00	3.23	20	.02	.01
80	.17	.09	100	.57	.25			
			10	.10	.10			
30	.03	.02						
80	.17	.09	10	.30	.30			
10	.01	.01						
90	25.50	6.01	100	71.70	8.64			
10	.01	.01						
			10	.01	.01			
90	12.0	3.00	100	23.3	6.79	100	100.0	0
100	6.4	.34	100	4.8	.42	80	1.0	.21

	0m MLLW			1.25m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Hasp	10	.20	.20			
Nesp				10	.10	.10
Myed	100	60.80	5.16	100	81.70	6.14
Hiar	10	.20	.20			
Cosp	100	31.20	4.95	100	20.00	3.76
Nope						
Lisi	20	.90	.80	70	8.60	6.84
Basp	70	3.15	2.98	90	2.51	.82
Bast	30	.03	.02	50	.05	.02
Gnor	10	.10	.10	30	.50	.27
Acsp						
Ulsp	80	1.13	.43	40	.53	.50
Ensp	10	.01	.01			
Fudi	30	.03	.02	70	4.00	1.58
Main	10	.01	.01			
Posp	20	.02	.01	10	.01	.01
Rhla				30	1.21	1.00
Ppsp	30	.12	.10			
Total Unoccupied Surface	100	35.8	5.86	90	17.0	5.32
Species Richness	100	5.0	.60	100	5.5	.52

Site # 18								
2.5m MLLW			3.75m MLLW			5m MLLW		
Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
100	33.40	5.97	60	4.04	3.05			
100	42.90	9.60	50	1.10	.46			
						10	.10	.10
100	414.00	70.87	100	370.80	87.17	100	77.80	52.67
100	54.60	5.54	100	59.80	7.60	50	2.31	1.30
90	.27	.12	80	.26	.12			
30	.12	.10						
20	.11	.10						
90	14.81	4.24	30	.80	.47	10	.01	.01
10	.01	.01						
100	12.7	2.07	100	36.0	7.41	100	97.7	1.30
100	5.5	.31	100	3.4	.31	100	1.7	.30

	Site # 19														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Nesp				10	.10	.10									
Myed	100	90.30	2.62	100	61.80	7.11	100	52.20	7.79	60	.44	.26			
Hiar	30	.90	.55												
Cosp	90	15.50	7.30	100	37.40	10.94	100	8.10	1.64	90	4.60	1.44			
Nope										20	.70	.60			
Lisi	50	.70	.30	100	31.50	10.30	100	419.00	115.22	100	280.00	55.66	100	46.10	13.27
Basp	30	.12	.10	100	.86	.40	100	32.00	8.00	100	42.50	8.00			
Bast	30	.03	.02	70	.07	.02	90	.18	.09	90	.09	.01			
Gnor	10	.40	.40	30	.50	.27									
Ulsp	70	1.02	.42	50	.24	.20									
Ensp				40	.04	.02									
Fudi	30	.31	.21	40	3.80	1.79	80	20.30	5.60	100	62.00	8.37			
Brsl				10	.10	.10									
Posp	10	.01	.01	10	.01	.01									
Rhla	10	.10	.10												
Total Unoccupied Surface	80	9.0	2.42	100	36.5	7.11	100	8.7	1.21	100	16.2	5.99	100	100.0	0
Species Richness	100	4.5	.54	100	5.9	.35	100	4.8	.13	100	4.7	.30	100	1.0	0

	Site # 20														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Myed	100	76.00	7.41	100	73.20	5.87	90	62.50	7.57	50	3.00	1.28			
Hiar	60	1.80	.68	30	.40	.22									
Cosp	100	24.30	3.68	100	24.40	2.77	100	14.30	4.64						
Nope										60	1.00	.39	20	.20	.13
Lisi	30	.30	.15	70	8.10	5.13	100	57.00	9.92	100	715.00	56.30	100	5.60	1.45
Seve	10	.20	.20												
Basp	90	3.32	1.13	100	2.90	.55	100	8.20	1.65	100	92.90	1.45	100	3.82	.90
Bast	90	.57	.33	80	.27	.19	100	11.04	9.68	100	2.31	.47	20	.02	.01
Gnor				10	.20	.20									
Acsp							30	.31	.21	20	.50	.40			
Ulsp	70	1.21	.49	50	1.11	.58	20	.21	.20						
Ensp							20	.11	.10						
Fudi	20	1.20	.81	40	1.30	.67	80	8.51	4.13	60	3.72	2.96	30	.41	.27
Total Unoccupied Surface	90	21.7	6.88	100	24.9	5.43	90	21.0	3.48	100	4.1	.80	100	95.9	.97
Species Richness	100	4.8	.20	100	5.0	.21	100	5.4	.31	100	4.0	.42	100	2.5	.27

	Site # 21*														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Nesp										10	.10	.10			
Myed				100	89.20	1.58	100	75.90	6.24	80	7.71	3.12			
Cosp				100	8.60	2.21	100	7.20	1.62	90	9.78	2.01			
Lisi				100	69.40	14.58	100	314.00	143.45	100	508.00	84.57	100	22.80	9.64
Basp				100	6.10	1.71	100	14.60	3.23	100	83.20	5.00	30	.03	.02
Bast				50	.05	.02	100	.29	.19	100	.48	.25			
Acsp				20	.02	.01	10	.01	.01						
Ulsp				20	.02	.01	10	.01	.01						
Ensp				20	.02	.01				50	.42	.22			
Grsl										10	.30	.30			
Fudi				100	12.20	3.01	100	25.00	4.71	90	7.52	3.17	10	.01	.01
Brfi				10	.01	.01	20	.30	.21	10	.01	.01			
Posp				20	.21	.20									
Rhla				10	.01	.01									
Ppsp				70	2.52	1.16	20	.11	.10						
Total Unoccupied Surface				100	4.7	.87	100	6.0	1.17	100	6.1	.94	100	100.0	0
Species Richness				100	6.7	.47	100	5.6	.22	100	5.3	.45	100	1.4	.16

	Site # 22														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Hasp	10	.50	.50	10	.10	.10									
Myed	100	67.50	4.17	100	60.00	7.13	100	68.70	5.07	90	7.32	2.52			
Hiar	50	.70	.26												
Cosp	100	25.70	3.31	100	36.70	2.44	100	32.00	12.15	80	5.70	1.73	10	.10	.10
Nope										10	.10	.10	20	.90	.80
Lisi	50	.50	.17	90	14.70	3.28	100	103.50	23.89	100	222.00	37.65	100	25.80	5.87
Mapu	10	.10	.10												
Basp	50	.14	.10	100	30.00	6.23	100	30.50	5.60	100	76.20	3.37	100	4.80	1.03
Bast	40	.04	.02	90	.18	.09	90	.09	.01	90	.09	.01	40	.04	.02
Gnor	50	1.40	.54	40	1.10	.53	40	.60	.27						
Idwo										10	.10	.10			
Ulsp	90	1.54	.57	50	.05	.02				20	.02	.01			
Ensp										10	.01	.01			
Fudi	10	.01	.01	50	.44	.40	100	9.12	3.39	100	56.50	10.83	80	1.06	.72
Posp				10	.50	.50									
Ppsp	70	2.32	.85												
Rhsp	10	.01	.01												
Total Unoccupied Surface	100	32.0	4.03	100	12.5	2.61	90	5.2	1.17	80	6.0	2.41	100	94.2	1.23
Species Richness	100	6.2	.29	100	5.5	.43	100	5.4	.16	100	5.2	.29	100	3.1	.28

	Site # 23														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Nesp	10	.10	.10				10	.20	.20	10	.10	.10			
Myed	100	33.90	9.95	90	39.30	11.52	100	70.10	10.01	90	3.74	1.94	10	.10	.10
Hiar	50	.80	.29	10	.10	.10									
Cosp	100	18.90	2.58	100	38.50	6.63	100	5.70	1.08	90	5.40	1.48			
Lisi	10	.10	.10	90	40.20	20.98	100	407.00	102.14	100	1200.00	120.19	100	374.00	108.84
Mapu	70	2.70	1.14												
Basp	100	12.31	3.40	100	23.20	8.04	100	15.41	4.59	100	72.50	7.72	90	16.91	7.36
Bast	100	.28	.12	90	.67	.49	70	.07	.02	90	.46	.21	20	.02	.01
Grcr	10	.10	.10	20	.80	.70									
Anpu	10	.10	.10												
Acsp				10	.01	.01	60	.15	.10						
Ulsp	100	12.50	3.15	60	2.44	1.99	20	.11	.10						
Ensp	10	.01	.01												
Fudi				30	4.00	3.47	100	25.01	7.39	100	29.50	8.10	40	5.02	4.01
Mein				10	.10	.10	40	.32	.21						
Alte	70	3.81	1.23												
Brfi				10	.01	.01									
Pcsp				20	.21	.20									
Rhla	30	.80	.51												
Ppsp	80	4.30	1.99	70	7.02	3.51	70	.64	.33						
Lisp	60	1.12	.60	30	.03	.02									

	Site # 23														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Total Unoccupied Surface	90	39.2	8.46	100	27.7	7.64	60	2.7	1.03	100	15.0	3.94	100	81.6	8.25
Species Richness	100	8.5	.40	100	6.5	.60	100	7.0	.39	100	4.9	.18	100	2.4	.22

	Site # 24														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Myed	100	83.80	5.63	100	88.70	2.26	80	33.60	8.65	30	1.11	.99			
Hiar	10	.10	.10												
Cosp	100	37.20	2.89	100	22.40	3.30	100	14.20	3.39	40	5.70	2.72			
Nope										30	.80	.42			
Lisi				100	11.10	.99	100	393.00	86.13	100	828.00	140.29	30	8.10	4.63
Rasp	100	3.32	.84	100	4.12	1.40	100	40.60	4.99	100	57.50	6.29			
Bast	60	.06	.02	60	.06	.02	80	.46	.26	80	.08	.01			
Gnor	30	.40	.22												
Ulsp	70	1.22	.53	10	.10	.10									
Grsl	30	.90	.53												
Fudi	50	1.00	.39	90	8.50	2.50	80	7.01	2.38	100	27.21	8.69			
Brfi	10	.30	.30												
Ppsp	70	2.90	1.04	30	.51	.34									
Lisp	40	.52	.34	30	.03	.02	10	.01	.01						
Total Unoccupied Surface	90	14.4	5.24	100	10.2	1.93	90	28.4	6.57	100	27.5	5.01	100	100.0	0
Species Richness	100	6.1	.55	100	5.6	.34	100	4.7	.26	100	4.0	.42	30	.3	.15

	Site # 25														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Nesp	10	.10	.10	10	.20	.20									
Brsp	10	.01	.01												
Myed	100	65.50	7.90	100	90.00	3.25	100	78.30	6.21	100	27.10	5.29			
Hiar	100	5.80	2.63	10	.20	.20									
Cosp	100	7.70	.83	100	6.20	1.17	90	3.50	.75	90	25.90	8.80	10	.70	.70
Lisi				100	6.40	2.68	100	113.50	48.55	100	330.00	86.04	100	391.00	69.85
Basp	50	.32	.15	100	5.60	3.30	100	15.71	3.26	100	54.00	6.36	50	1.72	1.09
Bast	90	.77	.51	40	.04	.02	70	.07	.02	100	.46	.15			
Anpu	20	.20	.13												
Acsp										20	.21	.20			
Ulsp	100	27.20	6.51	30	.03	.02									
Fudi	10	.01	.01	80	5.92	3.30	90	22.40	6.93	100	63.50	5.92	90	11.31	4.25
Mein	20	.20	.13												
Lasp	40	.92	.60												
Alte	20	4.00	3.06												
Brfi				20	.20	.13									
Fosp	80	15.10	4.44	40	12.50	5.34	40	2.00	1.06						
Ppsp	100	26.00	4.07	20	3.50	2.59									
Irsp	10	.20	.20												
Lisp	40	.04	.02	10	.01	.01									

Species	0m MLLW Freq.(%)	0m MLLW Mean	0m MLLW S.E.	1.25m MLLW Freq.(%)	1.25m MLLW Mean	1.25m MLLW S.E.	2.5m MLLW Freq.(%)	2.5m MLLW Mean	2.5m MLLW S.E.	3.75m MLLW Freq.(%)	3.75m MLLW Mean	3.75m MLLW S.E.	5m MLLW Freq.(%)	5m MLLW Mean	5m MLLW S.E.
	Site # 25														
Total Unoccupied Surface	60	5.6	2.50	80	5.5	1.38	70	4.7	1.33	80	3.6	.75	100	87.1	4.18
Species Richness	100	8.5	.48	100	6.2	.42	100	5.2	.25	100	5.1	.18	100	2.5	.22

	0m MLLW			1.25m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Myed				90	2.75	1.31
Cosp				90	9.50	3.07
Lisi				100	62.10	21.25
Thli				10	.80	.80
Basp				100	47.00	10.32
Bast				70	2.61	.99
Amsp				20	.40	.31
Gnor				10	.10	.10
Idre				20	.20	.13
Idwo						
Acsp				100	42.21	11.84
Ulsp				70	4.91	1.95
Ensp				10	.10	.10
Fudi				20	.40	.27
Posp				40	.04	.02
Rhla						
Ppsp				10	.10	.10
Haam				10	.10	.10
Rhsp				40	2.30	1.09
Irsp				20	.60	.40
Crsp				20	.21	.20

Site # 26*								
2.5m MLLW			3.75m MLLW			5m MLLW		
Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
100	78.70	10.31	80	8.50	3.79			
100	15.90	8.66	100	43.00	19.16			
100	209.30	86.00	100	761.00	63.48	100	137.80	52.01
40	.70	.34						
100	32.70	7.41	100	67.60	4.70	60	10.92	6.73
100	2.03	.59	80	4.30	.83	40	.62	.40
10	.10	.10						
10	.10	.10	10	1.00	1.00			
10	.01	.01						
40	5.51	3.02	100	20.10	7.39	10	.01	.01
			10	.30	.30			
			10	.10	.10			

Site # 26*															
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Lisp				20	.02	.01									
Total Unoccupied Surface				100	12.7	2.76	40	4.3	2.30	100	14.2	1.99	100	88.5	7.12
Species Richness				100	8.0	.76	100	5.1	.23	100	5.1	.35	100	1.7	.21

	Site # 27*														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Nesp							10	.50	.50	10	.20	.20			
Myed				90	2.02	.68	100	41.50	6.41	100	49.00	6.09	50	.72	.49
Cosp				100	14.90	2.67	100	135.00	38.51	100	108.00	16.85	20	.40	.31
Nope													90	9.40	2.36
Lisi				40	1.90	1.09	100	254.50	84.22	100	503.00	99.15	100	160.50	22.12
Thli				10	.10	.10	80	3.80	1.13						
Theg							10	.30	.30						
Mapu							10	.10	.10						
Onbo							30	2.40	2.08						
Evtr				10	.10	.10	20	.20	.13						
Basp				100	.93	.22	100	28.00	6.29	100	8.70	1.74	100	17.41	4.29
Bast				100	.37	.14	70	.56	.49	100	.38	.20	70	.25	.13
Goma							10	.10	.10						
Acsp				80	10.60	3.50	80	1.34	.71	20	.02	.01	10	.01	.01
Ulsp				60	.91	.31									
Fudi				50	.05	.02	100	36.70	11.25	100	46.90	8.78	100	11.91	3.32
Mein				10	.10	.10									
Brfi				10	.01	.01									
Rhla							20	.20	.13						
Ppsp							10	.10	.10						
Gisp				30	.03	.02	30	.22	.20						

	Site # 27*														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Total Unoccupied Surface				100	87.2	3.67	90	16.7	4.76	90	17.5	2.71	100	73.8	6.08
Species Richness				100	5.9	.53	100	8.0	.47	100	5.3	.15	100	4.7	.34

	Site # 28*														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Myed				20	.02	.01	100	42.50	6.84	100	38.30	10.23	10	.20	.20
Cosp				100	10.30	1.94	100	65.80	17.35	100	36.30	16.96	10	.10	.10
Nope													10	1.00	1.00
Lisi				10	.10	.10	100	196.30	54.32	100	255.00	42.75	100	121.30	28.60
Thli				20	.20	.13	80	11.00	4.03						
Theg							10	.20	.20						
Mapu				10	.10	.10									
Evtr				10	.10	.10	10	.10	.10						
Basp				80	.27	.19	90	19.90	6.64	100	19.01	5.36	30	.41	.30
Bast				100	.28	.12	60	1.14	.82	100	14.00	2.33	30	.03	.02
Gnor													10	.10	.10
Pasp							10	.10	.10						
Acsp				80	3.41	1.01	60	.06	.02	10	.01	.01			
Ulsp				60	6.63	5.95	10	.01	.01						
Ensp							10	.01	.01	20	.02	.01	20	4.50	3.20
Grsl													10	.30	.30
Fudi							80	13.00	3.43	100	23.20	6.90			
Brfi				20	1.01	1.00									
Rhla							70	2.12	1.02						
Lisp				10	.50	.50									

	Site # 28*														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.F.
Total Unoccupied Surface				100	88.9	6.20	100	30.0	3.42	90	21.0	4.82	100	94.[illegible]	3.08
Species Richness				100	4.4	.52	100	7.2	.39	100	5.3	.15	100	2.1	.28

	Site # 29														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Nesp	10	.10	.10												
Myed	90	61.00	9.24	100	89.60	5.21	100	52.50	5.18	80	12.81	7.09			
Hiar	100	9.90	2.96												
Cosp	100	103.20	13.65	100	63.20	15.95	100	29.90	4.00	80	8.00	3.42	10	.20	.20
Nope										20	.40	.27	30	2.20	1.69
Lisi	10	.20	.20	100	21.30	8.97	100	139.30	33.57	100	283.00	63.86	100	167.20	47.01
Thli	90	2.50	.56	50	1.40	.58	70	1.60	.45	20	1.70	1.59			
Theg	10	.10	.10	10	.01	.01									
Stdr	10	.10	.10												
Basp	20	.02	.01	60	.25	.20	100	25.50	3.93	100	59.00	6.89			
Bast							90	1.05	.41	100	2.50	.50	20	.02	.01
Gnor	20	.60	.40												
Acsp				10	.10	.10									
Ulsp	70	.25	.13	10	.01	.01									
Ensp				10	.01	.01									
Fudi	20	.02	.01	30	1.71	1.49	70	3.80	1.53	60	8.60	7.39	10	.01	.01
Soul				10	1.00	1.00									
Posp	20	.02	.01							10	.01	.01			
Phla				20	3.10	2.99				30	1.40	.99			
Ppsp	20	.02	.01	10	.10	.10									
Haam				10	.20	.20									

	Site # 29														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.F.	Freq.(%)	Mean	S.E.
Lisp	30	1.80	1.48												
Total Unoccupied Surface	100	37.5	8.21	70	6.4	2.83	100	22.7	3.39	100	22.1	4.12	100	100.0	0
Species Richness	100	6.1	.41	100	5.2	.71	100	5.4	.16	100	5.0	.45	100	1.7	.26

	Site # 30														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Anel							10	.10	.10						
Nesp	10	.10	.10	20	.40	.27	10	.10	.10	30	.40	.22			
Katu				60	1.20	.44									
Toli	10	.10	.10												
Myed				20	.80	.55	90	64.20	11.16	90	8.00	1.81			
Hiar	100	6.80	2.09	70	2.30	.63									
Cosp	10	.10	.10	100	51.40	18.93	100	18.10	4.14	100	22.40	8.15			
Nope										50	1.20	.53			
Lisi	20	.20	.13	100	150.00	33.80	100	162.00	32.00	100	468.00	43.48	100	151.90	33.68
Thli	20	.20	.13	40	2.20	1.12	90	3.30	.90	20	.20	.13			
Theg				30	.12	.10	20	.11	.10						
Evtr	20	.20	.13	40	.40	.16									
Stdr	60	3.30	1.50												
Basp	20	.02	.01	10	.20	.20	80	4.61	2.86	100	11.40	1.41	40	.13	.10
Bast				80	1.34	.64	100	.19	.09	90	6.31	1.40			
Amsp										10	.10	.10			
Pasp				10	.10	.10									
Acsp				100	28.00	4.16	80	1.53	.70						
Ulsp	60	.73	.36	80	4.01	1.87	10	.01	.01						
Fudi				90	11.40	3.43	90	17.20	6.64	100	66.00	9.36			
Soul				30	.03	.02	20	.11	.10						

	Site # 30														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Mein				80	3.31	1.03									
Brfi				20	.60	.50									
Posp				10	.01	.01									
Rhla				80	4.20	1.17	70	8.40	3.96	30	.12	.10			
Ppsp	10	.01	.01	40	1.71	1.48	20	.51	.50						
Gisp	20	.02	.01	100	18.30	3.74									
Lisp	70	3.00	1.02	70	1.82	.85									
Total Unoccupied Surface	100	96.3	1.22	100	24.5	7.87	80	15.5	9.50	100	20.2	6.52	100	100.0	0
Species Richness	100	4.3	.68	100	12.5	.65	100	7.9	.38	100	6.3	.37	100	1.4	.16

	Site # 31														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Myed	80	.55	.30	90	8.73	5.01	100	23.70	6.00	60	.06	.02			
Hiar				20	.60	.43									
Cosp	100	3.70	.40	100	13.40	3.46	100	46.50	16.00	100	18.20	2.07			
Nope										100	3.80	.68			
Lisi	10	.10	.10	90	18.40	7.37	100	478.00	57.60	100	145.50	21.43	100	89.70	36.13
Thli				40	1.50	.89	50	1.60	.82	70	2.50	.82			
Mapu	70	1.50	.52												
Basp	80	.36	.20	100	2.84	1.05	100	71.60	6.41	100	17.20	1.87	50	.71	.33
Bast	90	.18	.09	100	.28	.12	50	.83	.55	100	2.21	.44	10	.01	.01
Acsp	20	.11	.10	60	.34	.21	20	.02	.01						
Ulsp	50	.14	.10	60	.35	.29									
Fudi				40	.04	.02	70	8.02	3.14	100	92.50	2.36	40	1.02	.73
Soul							40	.81	.41						
Brsl	80	.62	.16	90	.09	.01									
Posp	10	.01	.01	10	.10	.10									
Rhla				20	.11	.10	60	4.70	1.69						
Ppsp				10	.01	.01									
Gisp							40	.62	.50						
Lisp	10	.10	.10												
Total Unoccupied Surface	100	99.3	.30	100	89.3	5.46	100	7.6	1.48	90	7.0	1.97	100	98.3	1.04

	Site # 31														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Species Richness	100	5.2	.33	100	7.3	.79	100	6.8	.65	100	6.3	.21	100	1.9	.31

	Site # 32*														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Hcsp				10	.10	.10									
Anel				10	.10	.10	10	.30	.30						
Nesp				10	.10	.10									
Myed				100	49.80	5.18	100	83.30	6.54	100	13.50	3.36			
Hiar				30	.40	.22									
Cosp				100	84.00	14.47	100	131.00	34.27	100	74.00	11.37	10	.10	.10
Lisi				100	92.00	9.40	90	141.00	43.75	100	326.00	75.19	100	202.00	31.30
Thli				100	6.30	1.08	80	3.20	.93	20	.40	.31			
Theg				40	.32	.21	10	.01	.01						
Mapu				40	.90	.59									
Basp				100	6.30	1.52	90	4.21	2.39	100	40.70	4.31	60	.25	.20
Bast				30	.03	.02	90	.57	.33	100	12.30	1.59			
Acsp				100	.01	0	40	.13	.10	10	.01	.01			
Ulsp				20	.02	.01									
Fudi				90	3.43	1.63	80	.57	.49	100	11.20	3.69	70	1.05	.80
Soul				20	.21	.20									
Posp				10	.01	.01									
Rhla				50	2.71	1.31	10	.01	.01						
Ppsp				90	3.92	1.92	30	1.40	.91						
Haam				20	.02	.01									
Gisp				40	.04	.02	20	.02	.01	60	.33	.15	10	.01	.01

	Site # 32*														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Crsp										10	.01	.01			
Total Unoccupied Surface				100	31.0	5.36	90	9.7	3.17	100	25.5	3.29	100	98.8	.85
Species Richness				100	10.4	.54	100	6.6	.52	100	6.0	.21	100	2.5	.37

	Site # 33														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Tecr				20	.20	.13	10	.20	.20						
Nesp				60	1.50	.50				10	.10	.10			
Brsp				100	3.11	.93									
Katu				80	.90	.18									
Toli	10	.10	.10												
Myed	30	.21	.13	20	.30	.21	100	49.00	7.88	100	18.00	3.00	10	.01	.01
Hiar	40	1.20	.51	90	4.50	.82									
Cosp	100	20.60	6.31	100	191.00	15.01	100	123.00	19.27	100	133.00	26.88	20	.20	.13
Nope							10	.10	.10						
Lisi	10	.30	.30	100	55.40	13.26	100	200.50	55.22	100	279.00	31.29	100	345.00	93.37
Thli	10	.10	.10	100	17.90	4.31	70	2.70	.90	60	1.30	.50			
Theg				50	.42	.22	10	.01	.01						
Mapu	90	12.10	2.69	10	.20	.20									
Onbo	10	.20	.20	70	2.20	.53									
Seve	10	.50	.50												
Evtr	10	.10	.10	40	.50	.22									
Stdr	10	.10	.10												
Basp	90	.96	.54	100	28.50	5.11	100	23.51	8.39	100	9.34	5.10	70	.07	.02
Bast	100	.38	.20	100	4.10	.46	100	5.93	2.06	100	4.84	2.10	70	.07	.02
Amsp				10	.10	.10									
Gnor	10	.10	.10												

	Site # 33														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Pasp	10	.30	.30	30	.40	.22	10	.10	.10	20	.20	.13			
Goma				10	.10	.10									
Olma	10	.10	.10												
Acsp	80	1.11	.31	80	2.22	.99									
Ulsp	90	.66	.33												
Fudi				100	8.51	1.24	100	14.91	3.19	100	73.10	10.39	60	7.21	2.89
Soul				100	.75	.25									
Mein	30	.03	.02	10	.01	.01									
Posp	10	.01	.01												
Rhla	20	.02	.01	100	55.00	6.41	80	3.50	.83	40	1.61	1.05			
Ppsp	30	.21	.13	30	.31	.21									
Gisp										40	1.20	.65	50	1.11	.52
Crsp										20	.40	.27			
Lisp	70	4.70	2.45	80	.65	.33									
Total Unoccupied Surface	100	91.8	2.41	100	11.4	1.48	100	19.3	3.55	90	9.5	2.17	100	91.7	3.13
Species Richness	100	7.9	.87	100	14.4	.40	100	6.9	.28	100	6.9	.35	100	3.2	.53

	Site # 34														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Hasp				50	.42	.22									
Anel	10	.10	.10												
Nesp										20	.20	.13			
Brsp	20	.20	.13												
Myed	100	24.50	4.11	100	49.50	6.73	100	91.00	2.96	100	35.50	2.93			
Hiar	100	33.20	9.44	100	26.40	6.39									
Cosp	90	33.80	6.38	100	94.50	14.93	90	21.50	6.09	100	9.70	1.67			
Lisi	80	4.80	1.84	90	5.50	.83	100	11.20	2.59	100	228.00	44.37	100	37.10	8.69
Thli	100	6.00	1.32	100	11.50	2.06	80	2.50	1.13						
Theg	70	.25	.13	60	.24	.13	10	.01	.01						
Mapu	50	2.50	.89												
Bies	10	.20	.20												
Onbo	10	.10	.10												
Seve	10	.10	.10												
Basp	80	3.62	1.61	100	24.50	2.41	100	4.31	.86	100	61.70	2.46	90	3.03	1.27
Bast	90	1.33	.49	90	.77	.46	80	.08	.01	80	.85	.50	20	.02	.01
Pasp				10	.10	.10									
Anpu				10	.10	.10									
Acsp	100	13.80	5.26	60	1.91	.83									
Ulsp	90	7.82	2.56	40	.04	.02	20	.02	.01						
Ensp							10	.01	.01						

	Site # 34														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Fudi	50	.54	.50	80	4.40	1.01	80	4.72	1.71	100	73.70	13.43	40	2.51	1.34
Brsl	30	.80	.47												
Rhla				20	.21	.20	10	.10	.10						
Ppsp	70	.71	.21	80	1.71	.74	30	.21	.13						
Rhsp	30	1.00	.56												
Gisp	70	2.50	.69												
Lisp	50	.14	.10	30	.03	.02									
Total Unoccupied Surface	100	52.4	5.14	90	24.2	5.28	70	5.6	1.61	30	2.5	1.34	100	94.5	2.49
Species Richness	100	11.6	.60	100	9.8	.49	100	6.2	.42	100	5.2	.13	100	2.3	.21

	Site # 35*															
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW			
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	
Nesp				20	.30	.21	30	.40	.22	10	.10	.10				
Myed				100	11.60	3.27	100	11.52	2.68	80	2.33	.82				
Cosp				100	18.10	3.35	100	10.00	2.07	70	1.70	.42				
Nope							20	.20	.20	90	6.20	2.76				
Lisi				100	615.00	73.43	100	365.00	40.17	100	200.00	39.44	90	53.00	19.70	
Thli				30	.40	.22	20	.30	.21							
Basp				100	40.00	6.99	100	13.20	3.35	100	3.90	1.12				
Bast				100	.01	0	90	.47	.26	100	2.71	.51				
Idwo							10	.10	.10							
Pasp				10	.10	.10										
Anpu							20	.30	.21							
Olma				10	.10	.10	10	.10	.10							
Acsp				20	.31	.30										
Ulsp				20	.21	.20	10	.01	.01							
Fudi				60	6.04	4.26	100	94.50	3.37	100	95.50	3.45				
Soul				40	.04	.02										
Mein										10	.01	.01				
Rhla				60	2.11	.75	20	.02	.01	10	.01	.01				
Ppsp				60	2.91	1.28	20	.50	.34							
Gisp				30	.12	.10	40	.70	.34	30	.61	.50				
Lisp							10	.01	.01							

	Site # 35*														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Total Unoccupied Surface				100	43.5	7.46	20	1.0	.67	30	3.0	2.00	100	100.0	0
Species Richness				100	7.6	.60	100	7.0	.45	100	6.0	.26	90	.9	.10

	Site # 36														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Hasp				30	.40	.22									
Tecr				10	.10	.10									
Nesp	30	.30	.15	10	.10	.10									
Myed	90	5.30	1.47	100	70.80	6.56	100	78.00	6.20	100	71.90	3.66	10	.01	.01
Hiar	70	4.80	1.44	50	1.00	.42									
Cosp	70	6.00	1.84	100	62.30	27.57	100	32.50	14.86	100	23.50	5.61			
Lisi				90	7.60	1.74	100	25.00	5.51	100	131.00	16.76	90	80.50	18.81
Thli	10	.10	.10	60	1.90	1.06	40	2.00	1.67						
Theg				40	.04	.02									
Seve	30	.12	.10												
Spbo				10	.50	.50									
Stdr	10	.40	.40												
Basp	60	.44	.26	90	7.02	3.09	90	12.20	4.36	100	7.70	1.13	100	11.20	3.43
Bast	50	.05	.02	50	.14	.10	60	.06	.02	90	.47	.30	30	.03	.02
Acsp				60	4.12	2.54	20	.02	.01	80	.26	.12			
Ulsp	100	1.83	.54	20	.11	.10	10	.01	.01						
Fudi				80	6.71	2.50	100	1.16	.57	80	13.40	3.96			
Soul				60	3.63	2.51	20	.02	.01						
Mein				10	.10	.10	10	.01	.01						
Brfi				20	.50	.40									
Brsl	10	.50	.50												

	Site # 36														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Rhla				60	4.90	2.36	30	.70	.50	20	.11	.10			
Ppsp				20	.20	.13				30	1.90	1.48			
Gisp				10	.01	.01									
Lisp	70	3.91	2.03	50	2.11	1.47									
Total Unoccupied Surface	100	88.8	2.75	60	13.6	5.31	80	10.7	3.63	100	22.4	2.98	100	82.8	3.43
Species Richness	100	5.6	.62	100	9.5	1.00	100	6.2	.42	100	6.1	.31	100	2.0	.15

	Site # 37*														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Hasp				10	1.00	1.00	10	.01	.01						
Tecr				10	.20	.20									
Nesp				20	.20	.13									
Katu				10	.10	.10									
Myed				80	37.50	10.14	100	73.80	6.22	100	28.50	5.78			
Hiar				100	33.70	8.35									
Cosp				100	127.00	28.40	100	58.40	19.56	100	63.00	12.00			
Lisi				100	75.50	14.42	100	48.00	7.16	100	247.00	46.60	100	151.50	16.77
Thii				90	12.30	2.99	70	3.20	1.16						
Theg				40	.72	.51	20	.02	.01						
Mapu				20	.90	.71									
Basp				90	16.00	4.27	100	3.35	1.46	100	12.50	2.91	90	7.40	4.77
Bast				70	.07	.02	70	.07	.02	100	1.37	.67	20	.02	.01
Amsp				10	.10	.10									
Gnor				10	.10	.10									
Anpu				20	.20	.20									
Goma							10	.10	.10						
Acsp				100	14.70	3.88	30	.22	.20	40	.42	.30			
Ulsp				50	.05	.02									
Fudi				100	8.62	2.19	80	2.52	1.03	100	36.00	10.92	20	3.10	2.99
Soul				60	1.82	.86	30	.03	.02						

	Site # 37*														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Mein				10	.10	.10									
Posp				60	.94	.79									
Rhla				90	31.70	12.22	90	14.41	5.41	10	.50	.50			
Ppsp				80	3.41	1.01	20	1.01	1.00						
Gisp				20	.51	.50									
Lisp				60	.72	.30									
Total Unoccupied Surface				80	10.8	3.28	90	17.7	5.37	100	31.1	7.66	100	91.6	5.76
Species Richness				100	13.0	.39	100	7.4	.58	100	5.5	.17	100	2.1	.18

	Site # 38*														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Tecr				20	.60	.43	10	.10	.10	10	.10	.10			
Nesp				20	.40	.31				10	.10	.10			
Brsp				10	.01	.01									
Katu				10	.10	.10									
Toli				10	.20	.20									
Myed				40	2.91	2.47	100	56.00	7.52	80	6.21	2.62	10	.50	.50
Hiar				20	.30	.21									
Cosp				100	92.70	21.63	100	56.00	8.84	100	54.00	10.13	30	2.20	1.98
Nope										30	3.20	2.98	40	4.00	2.94
Lisi				100	141.50	41.83	100	97.00	19.15	100	122.00	20.10	100	101.00	13.20
Thli				50	5.30	2.96	50	1.10	.43	20	.40	.27			
Theg				10	.10	.10									
Mapu				50	1.80	.85									
Evtr				20	.40	.27									
Basp				20	.30	.21	20	.80	.55	30	1.11	.99	30	.03	.02
Bast				100	28.50	8.29	100	1.24	.43	90	14.10	4.48	70	1.53	.66
Pasp				30	.50	.27	10	.10	.10	10	.70	.70			
Anpu										10	.10	.10			
Acsp				50	3.70	2.43	20	.30	.21						
Ulsp				70	6.41	3.59									
Ensp				10	.10	.10				20	.11	.10			

	Site # 38*														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Fudi				90	5.60	2.79	100	21.52	5.37	100	63.01	10.80	80	19.31	9.02
Soul				30	.12	.10	10	.01	.01	10	.50	.50			
Posp				30	.60	.34									
Phla				90	16.10	4.58	10	.01	.01	10	.50	.50			
Ppsp				70	9.20	5.76	40	5.30	2.95	40	4.21	2.64			
Haam				40	.22	.13	20	.02	.01	10	.01	.01			
Gisp				30	1.01	.67				40	1.21	.81	40	1.30	.62
Crsp				10	.10	.10	10	.01	.01						
Lisp				60	13.02	6.50	10	.10	.10						
Total Unoccupied Surface				90	18.2	5.91	80	21.0	3.86	90	20.5	5.84	100	79.8	9.06
Species Richness				100	11.7	.90	100	6.9	.55	100	7.0	.73	100	3.8	.55

	Site # 39															
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW			
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Nesp				20	.30	.21				30	.50	.27			
Myed	90	48.00	10.36	100	50.50	8.21	100	83.60	6.97	90	6.01	1.32			
Hiar	100	13.50	4.59	90	14.50	6.84									
Cosp	100	62.60	14.73	100	168.50	33.71	100	82.10	45.67	100	42.80	9.82			
Lisi	40	1.00	.52	100	28.80	5.75	100	37.60	9.83	100	283.70	62.23	100	36.10	9.58
Thli	100	2.70	.58	100	19.00	3.81	80	7.20	3.48	50	.70	.26			
Theg				30	.03	.02									
Buba	30	.30	.15	40	.90	.43									
Mapu	40	.50	.22												
Evtr	10	.10	.10												
Stdr	20	.20	.13												
Basp	60	1.22	.55	100	8.72	2.75	90	3.35	2.46	100	35.50	2.73	10	.01	.01
Bast	70	.07	.02	90	1.55	.75	100	.47	.21	100	3.32	.95			
Idwo													30	.50	.31
Pasp				20	.20	.13									
Acsp	20	.21	.20	60	.24	.13	10	.01	.01						
Ulsp	10	.20	.20												
Fudi				90	6.82	3.79	80	12.30	5.74	100	51.00	9.12			
Soul				40	.23	.20									
Posp	20	.02	.01												
Rhla				100	14.21	4.61	30	.41	.30						

	Site # 39														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Haam				20	.02	.01									
Gisp										20	.50	.34			
Lisp				20	.02	.01									
Total Unoccupied Surface	100	50.6	10.01	100	23.4	4.06	60	5.8	2.22	100	26.0	5.10	100	100.0	0
Species Richness	100	6.6	.48	100	10.0	.37	100	6.0	.33	100	5.9	.35	100	1.4	.16

	Site # 40														
	0m MLLW			1.25m MLLW			2.5m MLLW			3.75m MLLW			5m MLLW		
Species	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
Nesp				10	.10	.10									
Myed				100	17.70	3.01	100	6.50	1.25						
Cosp				100	61.90	11.16	100	30.90	3.15	30	.90	.60			
Nope							100	12.60	3.30	40	1.50	.90			
Lisi				100	166.00	26.21	100	157.00	27.12	100	43.10	9.36			
Thli				60	1.30	.52	50	.60	.22						
Basp				100	12.20	5.20	100	15.00	2.49	20	.11	.10			
Bast				100	4.90	1.35	100	7.40	1.56	40	.53	.50			
Fudi				100	9.31	2.79	100	31.50	1.83	90	12.70	4.41			
Gisp				100	.86	.34	90	5.51	1.53	100	16.50	3.34			
Crsp				70	3.71	1.25	90	8.50	1.83						
Total Unoccupied Surface				100	54.5	5.08	100	42.5	4.73	100	70.8	5.86	100	100.0	0
Species Richness				100	7.4	.16	100	8.3	.26	100	4.0	.42	0	0	0

Appendix VII. Pooled species richness (mean number of species per quadrat) data, combining four vertical intertidal levels (1.25-5 m MLLW) and five levels (0-5 m MLLW) for 40 sites and 30 sites, respectively. "-" indicates that the 0 m level was not sampled.

	4 intertidal levels (n=40)			5 intertidal levels (n=50)		
Site #	Freq.(%)	Mean	S.E.	Freq.(%)	Mean	S.E.
1	67.5	1.58	.23	74.0	1.96	.22
2	92.5	2.38	.17	94.0	2.40	.15
3	80.0	2.93	.31	84.0	3.00	.25
4	75.0	3.90	.41	80.0	4.04	.33
5	75.0	2.63	.29	-	-	-
6	80.0	3.48	.34	84.0	3.38	.28
7	85.0	2.32	.22	84.0	2.22	.19
8	80.0	4.43	.43	84.0	4.52	.35
9	92.5	4.80	.38	94.0	4.86	.32
10	97.5	3.38	.24	98.0	3.40	.20
11	100	4.35	.29	100	4.42	.24
12	92.5	3.85	.24	94.0	3.88	.21
13	100	3.85	.25	100	3.88	.21
14	100	3.95	.23	100	4.24	.21
15	100	4.25	.32	100	4.42	.27
16	100	4.03	.17	100	3.94	.15
17	95.0	4.78	.40	96.0	4.92	.33
18	100	4.05	.31	100	4.24	.28
19	100	4.10	.32	100	4.18	.28
20	100	4.23	.23	100	4.34	.19
21	100	4.75	.36	-	-	-
22	100	4.80	.22	100	5.08	.20
23	100	5.20	.34	100	5.78	.33
24	82.5	3.65	.36	86.0	4.14	.33
25	100	4.75	.26	100	5.50	.31
26	100	4.95	.42	-	-	-
27	100	6.00	.28	-	-	-
28	100	4.78	.35	-	-	-
29	100	4.35	.33	100	4.72	.29
30	100	7.13	.68	100	6.56	.58
31	100	5.58	.43	100	5.50	.35
32	100	6.50	.53	-	-	-
33	100	7.98	.71	100	7.96	.59
34	100	6.03	.49	100	7.30	.55
35	97.5	5.38	.47	-	-	-
36	100	6.03	.53	100	5.94	.44
37	100	7.15	.69	-	-	-
38	100	7.33	.56	-	-	-
39	100	5.90	.53	100	6.04	.43
40	75.0	4.93	.54	-	-	-

Appendix VIII. Pooled total unoccupied substrate surface (%) data, combining four vertical intertidal levels (1.25-5 m MLLW) and five levels (0-5 m MLLW) for 40 sites and 30 sites, respectively. "-" indicates that the 0 m MLLW level was not sampled.

Site #	4 intertidal levels (n=40) Freq.(%)	Mean	S.E.	5 intertidal levels (n=50) Freq.(%)	Mean	S.E.
1	100	79.53	3.66	80.0	63.62	5.40
2	100	73.00	4.14	100	73.90	3.49
3	100	79.55	2.77	100	75.20	2.76
4	100	53.05	5.71	100	52.60	4.87
5	95.0	61.00	5.54	-	-	-
6	100	64.43	4.34	100	60.70	3.76
7	100	66.13	4.27	100	71.70	3.80
8	100	66.33	4.69	100	62.14	4.20
9	100	56.98	5.23	100	52.70	4.64
10	97.5	48.93	5.84	98.0	48.34	4.87
11	100	51.53	5.17	100	51.62	4.19
12	100	45.63	5.30	100	40.30	4.54
13	100	36.65	5.99	98.0	32.82	5.07
14	92.5	51.23	5.59	94.0	50.36	4.59
15	85.0	36.65	6.59	88.0	34.18	5.44
16	100	52.63	5.13	100	50.74	4.58
17	97.5	37.85	6.12	98.0	36.04	5.05
18	97.5	40.85	5.89	98.0	39.84	4.84
19	100	40.35	6.18	96.0	34.08	5.26
20	97.5	36.60	5.85	96.0	33.62	4.92
21	100	29.20	6.56	-	-	-
22	92.5	29.48	6.08	94.0	29.98	4.91
23	90.0	31.75	5.61	90.0	33.24	4.78
24	97.5	41.53	5.89	96.0	36.10	5.05
25	82.5	25.23	5.83	78.0	21.30	4.81
26	85.0	29.93	5.80	-	-	-
27	95.0	48.80	5.57	-	-	-
28	97.5	58.63	5.77	-	-	-
29	92.5	37.80	6.02	94.0	37.74	5.06
30	95.0	40.05	6.50	96.0	51.30	6.10
31	97.5	50.55	7.10	98.0	60.30	6.31
32	97.5	41.25	5.73	-	-	-
33	97.5	32.98	5.61	98.0	44.74	5.62
34	72.5	31.70	6.14	78.0	35.84	5.14
35	62.5	36.88	6.70	-	-	-
36	85.0	33.88	5.46	88.0	44.86	5.40
37	90.0	37.35	5.83	-	-	-
38	90.0	34.88	5.18	-	-	-
39	90.0	38.80	6.02	92.0	41.16	5.22
40	100	66.95	4.08	-	-	-

Appendix IX. Pooled silt ≧ 0.5 cm thickness (% cover) data, combining four vertical intertidal levels (1.25-5 m MLLW) and five levels (0-5 m MLLW) for 40 sites and 30 sites, respectively. "-" indicates that the 0 m level was not sampled.

Site #	4 intertidal levels (n=40) Freq.(%)	Mean	S.E.	5 intertidal levels (n=50) Freq.(%)	Mean	S.E.
1	0	0	0	0	0	0
2	55.0	3.13	.65	54.0	3.06	.56
3	15.0	1.00	.41	28.0	3.80	1.14
4	7.5	.45	.28	12.0	.96	.47
5	22.5	3.05	1.07	-	-	-
6	37.5	3.88	1.36	46.0	4.90	1.22
7	20.0	2.75	1.03	24.0	2.94	.90
8	2.5	.25	.25	15.0	.90	.37
9	10.0	.78	.46	22.0	1.54	.50
10	5.0	.33	.26	20.0	1.50	.50
11	20.0	1.68	.64	22.0	2.14	.68
12	10.0	.50	.24	26.0	2.10	.55
13	5.0	.45	.38	10.0	.66	.35
14	7.5	.35	.20	6.0	.28	.16
15	0	0	0	10.0	.54	.23
16	17.5	1.00	.37	30.0	2.54	.78
17	2.5	.13	.13	10.0	.50	.21
18	10.0	.43	.21	14.0	.64	.23
19	2.5	.13	.13	2.0	.10	.10
20	10.0	.75	.42	12.0	.76	.35
21	2.5	.13	.13	-	-	-
22	7.5	.33	.19	24.0	1.66	.54
23	0	0	0	6.0	.24	.14
24	2.5	.50	.50	4.0	.54	.42
25	0	0	0	0	0	0
26	0	0	0	-	-	-
27	0	0	0	-	-	-
28	0	0	0	-	-	-
29	2.5	.13	.13	2.0	.10	.10
30	0	0	0	0	0	0
31	0	0	0	0	0	0
32	0	0	0	-	-	-
33	0	0	0	0	0	0
34	0	0	0	0	0	0
35	0	0	0	-	-	-
36	0	0	0	0	0	0
37	0	0	0	-	-	-
38	0	0	0	-	-	-
39	0	0	0	0	0	0
40	0	0	0	-	-	-

Appendix X. Results of stepwise multiple regressions of individual species distributions (using coverage/abundance data) against all environmental parameters measured (including sampling date and excluding air temperature and 1% light depth). See Table 3 for meanings of abbreviated species names. Results are organized by vertical intertidal level (0-5 m MLLW); each level contains results computed from one data set containing suspended particulate carbon and nitrogen measurements and from another data set that does not include those measurements. Thus, results from the 0 m and 1.25 m levels appear first, followed by 2.5 m and 3.75 m results, and finally 5 m results. Values are the coefficients of correlation (*r*) at that intertidal level between the distributional pattern of a given species and the associated environmental parameter. "-" indicates that the species was not encountered at that intertidal level; "X" indicates that the species was present but its distributional pattern showed no significant correlation with any environmental variable in the analysis (critical *F* = 4.000). For each species, all significantly correlated environmental variables are listed "stepwise", in decreasing order of correlation strength. Results also are shown for species richness (mean number of species per quadrat) and percent total unoccupied surface.

Species	Vertical Intertidal Level (data set)			
	0m MLLW (no CN data)	0m MLLW (incl. CN data)	1.25m MLLW (no CN data)	1.25m MLLW (incl. CN data)
Hasp	X	X	Aspect (.1330)	Aspect (.2773) Partic. C % wt. (.4081)
Hcsp	-	-	Slope (.1573)	X
Anel	Distance/Age (.1632)	Distance/Age (.2478)	Slope (.1573)	X
Tecr	-	-	Distance/Age (.1325)	Distance/Age (.2348)
Nesp	X	X	Water Temp. (.1911) Aspect (.2763)	Salinity (.2091)
Brsp	X	X	X	X
Katu	-	-	Water Temp. (.1404) Aspect (.2510)	Salinity (.2165) Aspect (.3784)
Toli	Water Temp. (.2073) Aspect (.4735)	Salinity (.2631) Aspect (.5242)	X	X
Myed	Tot. Partic. mg/L (.1667) Water Temp. (.4070) Distance/Age (.5036)	X	X	Aspect (.1854)
Hiar	Distance/Age (.1806)	X	Distance/Age (.3878)	Distance/Age (.2069)
Cosp	X	X	Distance/Age (.3348)	Distance/Age (.2485)

Species	Vertical Intertidal Level (data set)			
	0m MLLW (no CN data)	0m MLLW (incl. CN data)	1.25m MLLW (no CN data)	1.25m MLLW (incl. CN data)
Nope	-	-	-	-
Lisi	Distance/Age (.1690)	Partic. N % wt. (.1715)	Distance/Age (.1761) Aspect (.2575)	X
Thli	Distance/Age (.2514)	X	Distance/Age (.3019)	Distance/Age (.2896)
Theg	X	X	Distance/Age (.1738)	Distance/Age (.2549)
Buba	Distance/Age (.1588)	X	X	X
Mapu	Water Temp. (.1837)	Distance/Age (.2182) Aspect (.3606)	Distance/Age (.1358)	Distance/Age (.1451)
Bies	X	X	-	-
Onbo	Distance/Age (.1517)	Distance/Age (.2321)	X	X
Seve	Water Temp. (.2171)	Water Temp. (.2715)	-	-
Spbo	-	-	X	X
Evtr	Water Temp. (.2732) Aspect (.4233)	Salinity (.2462) Aspect (.4914)	Water Temp. (.1862) Aspect (.4010)	Water Temp. (.2107) Aspect (.4322)
Stdr	Water Temp. (.1524) Aspect (.2749)	Salinity (.1699)	-	-

Species	Vertical Intertidal Level (data set)			
	0m MLLW (no CN data)	0m MLLW (incl. CN data)	1.25m MLLW (no CN data)	1.25m MLLW (incl. CN data)
Basp	Distance/Age (.3090)	Distance/Age (.3999) Water Temp. (.5088)	X	X
Bast	Slope (.1919)	Distance/Age (.2044)	Distance/Age (.1194)	Water Temp. (.2033)
Amsp	-	-	X	C:N Ratio (.2056) No. Ice Frag. (.6659)
Gnor	X	X	X	X
Idre	-	-	X	X
Idwo	-	-	-	-
Pasp	X	X	Distance/Age (.1872) Aspect (.1238)	Salinity (.2000)
Anpu	Slope (.2488)	X	X	Aspect (.1798)
Goma	-	-	X	X
Olma	X	X	X	X
Acsp	X	X	X	Water Temp. (.2287)
Ulsp	Slope (.2502)	Partic. C % wt. (.3814)	Water Temp. (.1702) Slope (.1130)	Partic. N % wt. (.2453)

Species	Vertical Intertidal Level (data set)			
	0m MLLW (no CN data)	0m MLLW (incl. CN data)	1.25m MLLW (no CN data)	1.25m MLLW (incl. CN data)
Uusp	X	X	Tot. Partic. mg/L (.1407) No. Ice Frag. (.7142) Sampling Date (.7616)	C:N Ratio (.2550) No. Ice Frag. (.8091) Tot. Partic. mg/L (.8626) Extinc. Coeff. (.8946) Salinity (.9210) Sampling Date (.9350)
Ensp	No. Ice Frag. (.9230) Extinc. Coeff. (.9451)	No. Ice Frag. (.9645)	No. Ice Frag. (.9448) Extinc. Coeff. (.9631) Tot. Partic. mg/L (.9725)	No. Ice Frag. (.9857) Partic. N mg/L (.9883)
Grsl	X	Sampling Date (.1770) Slope (.3782)	Salinity (.1323) Slope (.2793)	X
Fudi	X	X	Salinity (.2974)	Water Temp. (.2842)
Soul	-	-	Water Temp. (.1537)	Distance/Age (.2000)
Mein	X	X	X	X
Lasp	Slope (.3687) Sampling Date (.4652)	X	-	-
Alte	Slope (.1322)	X	-	-
Brfi	X	X	X	X
Brsl	No. Ice Frag. (.9598) Extinc. Coeff. (.9777) Tot. Partic. mg/L (.9849)	No. Ice Frag. (.9864)	No. Ice Frag. (.9600) Ext. Coeff. (.9887) Tot. Partic. mg/L (.9844)	No. Ice Frag. (.9868) Partic. N mg/L (.9889)

Species	Vertical Intertidal Level (data set)			
	0m MLLW (no CN data)	0m MLLW (incl. CN data)	1.25m MLLW (no CN data)	1.25m MLLW (incl. CN data)
Posp	Slope (.3429) Sampling Date (.4491)	X	X	X
Rhla	X	X	Water Temp. (.1924)	Distance/Age (.1812)
Ppsp	Slope (.3329)	Partic. C % wt. (.2584)	Salinity (.1317) Aspect (.2453)	Partic. C % wt. (.2504)
Haam	-	-	Sampling Date (.1128)	X
Rhsp	X	X	X	X
Irsp	Slope (.3687) Sampling Date (.4652)	X	X	X
Gisp	X	X	X	X
Crsp	-	-	Distance/Age (.1206) Water Temp. (.2457)	X
Lisp	Water Temp. (.3774) Aspect (.4697)	Water Temp. (.4370) Aspect (.5532)	Distance/Age (.0958) Aspect (.1856)	Water Temp. (.3091)
Species Richness	Distance/Age (.4443)	Partic. N % wt. (.5106)	Distance/Age (.6058)	Distance/Age (.6194)
Total Unoccupied Surface	Water Temp. (.2795) Distance/Age (.4494)	Salinity (.5051)	X	X

Species	Vertical Intertidal Level (data set)			
	2.5m MLLW (no CN data)	2.5m MLLW (incl. CN data)	3.75m MLLW (no CN data)	3.75m MLLW (incl. CN data)
Hasp	X	X	-	-
Hcsp	-	-	-	-
Anel	Slope (.1616)	X	-	-
Tecr	X	X	X	X
Nesp	X	X	Water Temp. (.1849)	Partic. N mg/L (.2119) Slope (.3385)
Brsp	-	-	-	-
Katu	-	-	-	-
Toli	-	-	-	-
Myed	Distance/Age (.3656)	Distance/Age (.4760) Sampling Date (.6263)	Water Temp. (.2522)	Distance/Age (.3615)
Hiar	-	-	-	-
Cosp	Distance/Age (.2485)	Partic. N % wt. (.2595)	Distance/Age (.2028)	Distance/Age (.2039)
Nope	Distance/Age (.1324) Water Temp. (.2847)	X	Distance/Age (.1460)	Salinity (.1710)
Lisi	Tot. Partic. mg/L (.1248)	Sampling Date (.2326) Tot. Partic. mg/L (.3946)	Extinc. Coeff. (.1043)	X

Species	Vertical Intertidal Level (data set)			
	2.5m MLLW (no CN data)	2.5m MLLW (incl. CN data)	3.75m MLLW (no CN data)	3.75m MLLW (incl. CN data)
Thli	Water Temp. (.3756)	Partic. N % wt. (.3736)	Water Temp. (.1768)	Salinity (.2686) Partic. C % wt. (.3838)
Theg	Water Temp. (.1094) Aspect (.2068)	Partic. N % wt. (.2285)	-	-
Buba	-	-	-	-
Mapu	X	Slope (.2026)	-	-
Bies	-	-	-	-
Onbo	X	Slope (.2026)	-	-
Seve	-	-	-	-
Spbo	-	-	-	-
Evtr	X	Partic. N % wt. (.1742)	-	-
Stdr	-	-	-	-
Basp	Water Temp. (.1205) Tot. Partic. mg/L (.3190)	X	X	X

Species	Vertical Intertidal Level (data set)			
	2.5m MLLW (no CN data)	2.5m MLLW (incl. CN data)	3.75m MLLW (no CN data)	3.75m MLLW (incl. CN data)
Bast	Water Temp. (.1014)	X	Water Temp. (.2216) Aspect (.3442)	Water Temp. (.2635) Aspect (.4139) Slope (.5544)
Amsp	Extinc. Coeff. (.4953) Tot. Partic. mg/L (.6826) Sampling Date (.7388)	X	Extinc. Coeff. (.3070) Salinity (.4039) Distance/Age (.4685) Tot. Partic. mg/L (.5470)	X
Gnor	X	X	X	X
Idre	-	-	-	-
Idwo	X	X	X	X
Pasp	Water Temp. (.1348) Aspect (.2872) Slope (.3753)	Partic. N % wt. (.1689)	X	X
Anpu	X	X	X	X
Goma	X	X	-	-
Olma	X	X	-	-
Acsp	Water Temp. (.1361) Aspect (.2282)	Slope (.1790)	Aspect (.1461)	Aspect (.2196)
Ulsp	Sampling Date (.1138)	X	X	X

Species	Vertical Intertidal Level (data set) 2.5m MLLW (no CN data)	2.5m MLLW (incl. CN data)	3.75m MLLW (no CN data)	3.75m MLLW (incl. CN data)
Uusp	Tot. Partic. mg/L (.1399) No. Ice Frag. (.7121) Sampling Date (.7608)	C:N Ratio (.2531) No. Ice Frag. (.8059) Tot. Partic. mg/L (.8601) Extinc. Coeff. (.8895) Salinity (.9175) Slope (.9326)	Tot. Partic. mg/L (.1407) No. Ice Frag. (.7131) Sampling Date (.7608)	C:N Ratio (.2552) No. Ice Frag. (.8091) Tot. Partic. mg/L (.8618) Extinc. Coeff. (.8938) Salinity (.9205) Sampling Date (.9346)
Ensp	No. Ice Frag. (.9662) Extinc. Coeff. (.9825) Tot. Partic. mg/L (.9886) Water Temp. (.9901)	No. Ice Frag. (.9946) Partic. N mg/L (.9959)	Salinity (.2203) No. Ice Frag. (.3041)	Salinity (.2681)
Grsl	X	Partic. N mg/L (.1607) Water Temp. (.3654) No. Ice Frag. (.4664)	X	X
Fudi	X	X	X	Distance/Age (.1884)
Soul	X	Salinity (.2068) Partic. C % wt. (.3262)	X	X
Mein	X	X	X	X
Lasp	-	-	-	-
Alte	-	-	-	-
Brti	Distance/Age (.1216) Salinity (.2918)	Distance/Age (.2003) C:N Ratio (.3648)	X	X

Species	Vertical Intertidal Level (data set): 2.5m MLLW (no CN data)	2.5m MLLW (incl. CN data)	3.75m MLLW (no CN data)	3.75m MLLW (incl. CN data)
Brsl	No. Ice Frag. (.9600) Extinc. Coeff. (.9773) Tot. Partic. mg/L (.9843)	No. Ice Frag. (.9868) Partic. N mg/L (.9889)	X	X
Posp	X	X	X	Partic. N mg/L (.1652) Water Temp. (.3481)
Rhla	Water Temp. (.2062)	Salinity (.2975)	Water Temp. (.1250)	Distance/Age (.1452)
Ppsp	Distance/Age (.1163) Aspect (.2338)	Distance/Age (.2459)	X	X
Haam	X	X	X	X
Rhsp	-	-	-	-
Irsp	-	-	-	-
Gisp	Distance/Age (.1605) Water Temp. (.2918)	Salinity (.1764)	Distance/Age (.1658) Water Temp. (.3184)	X
Crsp	Distance/Age (.1292) Water Temp. (.2821)	X	X	X
Lisp	X	Sampling Date (.1720)	-	-
Species Richness	Distance/Age (.4614) Extinc. Coeff. (.5431)	Water Temp. (.5125) C:N Ratio (.6432) Partic. N mg/L (.7230)	Tot. Partic. mg/L (.4019) Salinity (.5866) Slope (.6396)	Tot. Partic mg/L (.4699) Salinity (.6501)

Species	Vertical Intertidal Level (data set)			
	2.5m MLLW (no CN data)	2.5m MLLW (incl. CN data)	3.75m MLLW (no CN data)	3.75m MLLW (incl. CN data)
Total Unoccupied Surface	Tot. Partic. mg/L (.3872) Distance/Age (.5209)	Distance/Age (.5476) Tot. Partic. mg/L (.6489)	Water Temp. (.3345) No. Ice Frag. (.4443)	Water Temp. (.5209) No. Ice Frag. (.6445)

Species	Vertical Intertidal Level (data set) 5m MLLW (no CN data)	5m MLLW (incl. CN data)
Hasp	-	-
Hcsp	-	-
Anel	-	-
Tecr	-	-
Nesp	-	-
Brsp	-	-
Katu	-	-
Toli	-	-
Myed	X	Partic. N % wt. (.1535)
Hiar	-	-
Cosp	X	Partic. N % wt. (.1630)
Nope	X	Slope (.1562)
Lisi	Water Temp. (.2175) Aspect (.3303)	Water Temp. (.3683) Partic. N mg/L (.4780)

Species	Vertical Intertidal Level (data set)	
	5m MLLW (no CN data)	5m MLLW (incl. CN data)
Thli	-	-
Theg	-	-
Buba	-	-
Mapu	-	-
Bies	-	-
Onbo	-	-
Seve	-	-
Spbo	-	-
Evtr	-	-
Stdr	-	-
Basp	Water Temp. (.1121) Sampling Date (.2108)	Partic. C % wt. (.2130)
Bast	X	Partic. N % wt. (.1706) Slope (.3348)
Amsp	-	-

Species	Vertical Intertidal Level (data set)	
	5m MLLW (no CN data)	5m MLLW (incl. CN data)
Gnor	X	Slope (.1777) Partic. N % wt. (.3302)
Idre	-	-
Idwo	X	X
Pasp	-	-
Anpu	-	-
Goma	-	-
Olma	-	-
Acsp	X	Slope (.2026)
Ulsp	-	-
Uusp	Extinc. Coeff. (.5731) Tot. Partic. mg/L (.8023) Distance/Age (.8594) Sampling Date (.8761)	X
Ensp	X	X
Grsl	X	Slope (.1777) Partic. N % wt. (.3302)

Species	Vertical Intertidal Level (data set)	
	5m MLLW (no CN data)	5m MLLW (incl. CN data)
Fudi	Aspect (.1172) Distance/Age (.2880)	Partic. N % wt. (.1962) Slope (.3492)
Soul	-	-
Mein	-	-
Lasp	-	-
Alte	-	-
Brfi	-	-
Brsl	-	-
Posp	-	-
Rhla	-	-
Ppsp	-	-
Haam	-	-
Rhsp	-	-
Irsp	-	-
Gisp	X	X

	Vertical Intertidal Level (data set)	
Species	5m MLLW (no CN data)	5m MLLW (incl. CN data)
Crsp	-	-
Lisp	-	-
Species Richness	Water Temp. (.2546)	Distance/Age (.2942) Sampling Date (.5212)
Total Unoccupied Surface	Water Temp. (.1590)	Partic. N % wt. (.2517) Sampling Date (.3816)

Appendix XI. Results of stepwise multiple regressions of principal component (PC) scores (generated by principal components analysis) of the biological data against all environmental parameters measured (including sampling date and excluding air temperature and 1% light depth). Results are given from the analyses of two data sets (with and without suspended carbon and nitrogen data) per vertical intertidal level. Values are the coefficients of correlation (r) for a given data set between a given PC score (PC1 through PC5) and the associated physical environmental parameter. "X" indicates that the PC score showed no significant correlation with any environmental parameter in the analysis (critical F = 4.000). For each PC score, all significantly correlated environmental variables are listed "stepwise", in decreasing order of correlation strength.

Vertical Intertidal Level (data set)	PC1	PC2
0m MLLW (no CN data)	X	Slope (.2775)
0m MLLW (incl. CN data)	X	Partic. N mg/L (.2964)
1.25m MLLW (no CN data)	Distance/Age (.0976)	X
1.25m MLLW (incl. CN data)	Partic. C % wt. (.4561)	X
2.5m MLLW (no CN data)	X	1)Distance/Age (.1430) 2)Water Temp. (.2723)
2.5m MLLW (incl. CN data)	Partic. N % wt. (.1432)	X

PC3	PC4	PC5
Water Temp. (.1529)	Salinity (.1886)	1)No. Ice Frag. (.9064) 2)Extinc. Coeff. (.9364)
Water Temp. (.1791)	1)Salinity (.2119) 2)Aspect (.3720)	1)No. Ice Frag. (.9493) 2)Salinity (.9600)
X	X	X
Aspect (.1829)	X	Distance/Age (.1875)
X	X	Water Temp. (.1768)
X	X	Water Temp. (.1648)

Vertical Intertidal Level (data set)	PC1	PC2
3.75m MLLW (no CN data)	1)Sampling Date (.0997) 2)Distance/Age (.1956) 3)Water Temp. (.3637)	Water Temp. (.1328)
3.75m MLLW (incl. CN data)	1)C:N Ratio (.1560) 2)No. Ice Frag. (.4272) 3)Partic. N % wt. (.5456)	Salinity (.1663)
5m MLLW (no CN data)	X	X
5m MLLW (incl. CN data)	X	Slope (.1513)

PC3	PC4	PC5
X	Distance/Age (.0952)	1)Tot. Partic. mg/l (.3512) 2)No. Ice Frag. (.2398)
Water Temp. (.1585)	1)Distance/Age (.1774) 2)Partic. C % wt. (.3149)	C: N Ratio (.[illegible]433)
X	Extinc. Coeff. (.3185)	Extinc. Coeff. (.1678)
X	Partic. C % wt. (.3722)	Water Temp. (.2206)

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